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THE FOOD PREFERENCE OF
CHROTOGONUS TRACHYPTERUS (BLANCHARD)
(ORTHOPTERA : ACRIDOIDEA : PYRGOMORPHIDAE)

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[Communicated by Dr. G. L. Arora, Punjab University, Hoshiarpur]

INTRODUCTION

ACRIDIDS, though polyphagous, show some preference for certain food-plants. Maxwell-Darling (1934) made a passing reference to the choice of food-plant by *Chrotogonus* sp. Isely (1944) studied the food-preferences of the American grass-hoppers and correlated them with the structure of their mandibles. Husain *et al.* (1946) experimented with the desert locust to find out whether a plant was eaten readily, reluctantly, or avoided altogether. Roonwal (1953) described in detail the food-preferences of the desert locust. Williams (1954) studied the food-preferences of some British Acridids. The present investigations were undertaken to obtain information on the feeding habits of *Chrotogonus trachypterus* (Blanchard), an important pest of young plants in the Punjab and other parts of India, and in Africa and the Middle East countries.

MATERIAL AND METHOD

A study was made of the order in which 39 species of plants, both cultivated and wild, of 21 families, were chosen. The grasshoppers used in the experiments were
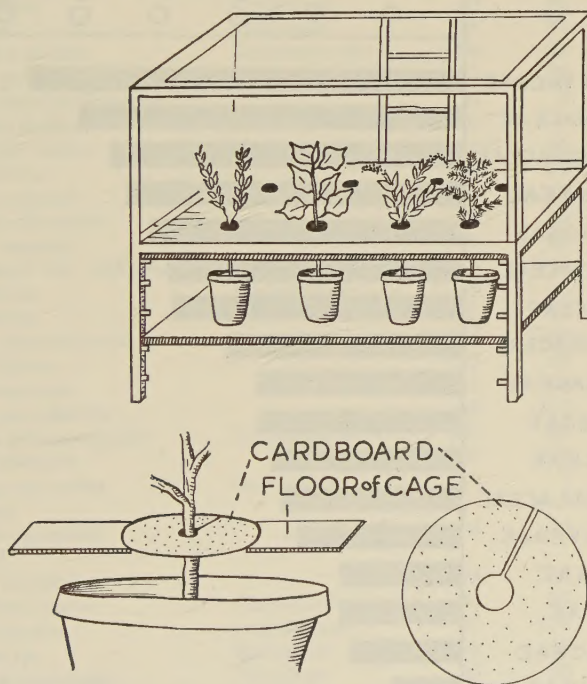
FIG. 1.—The experimental cage for estimating order of preference of various plants.

adults, reared in the laboratory from nymphs collected in the field. The cage used for estimating the order of preference of various plants (fig. 1) measured $75 \times 40 \times 30$ cm. and was mounted on legs 30 cm. high. The sides and top were of wire-gauze and the floor was of a metallic sheet with eight perforations of 3 cm. diameter, each in two rows. The plants tested were all mature ones grown in small flower-pots.

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Each plant was passed through the basal perforation into the cage, the flower-pot remaining outside supported on a wooden board of adjustable height. The escape of the grasshoppers was prevented by covering each perforation with a piece of cardboard with an opening in the centre large enough to allow the stem of the plant to pass through. The insects were thus brought into direct contact with the different plants. A common local weed, *Heliotropium eichwaldi* (Boraginaceae), served as the standard with which the remaining plants were compared. The cage was occupied by four species of plants, one the standard and three others, each occupying two different places, and 100 adults, starved previously for 20 hours, were introduced. The grasshoppers, after a few exploratory bites, started to feed on the plant of their choice. The number of adults feeding on different plants was noted after five minutes. Three such counts were taken at five minute intervals. As the majority of the adults stopped feeding after 15 minutes, no counts were taken beyond that time. Each experiment was repeated three times with three separate lots of grasshoppers and with the same four species of plants, but each time the plants occupied different positions in the cage. The order of preference for each plant was calculated by assuming the number of adults feeding on the standard plant to be 100 and calculating the corresponding number of adults feeding on the other plants. The order of preference for all the plants was thus calculated.
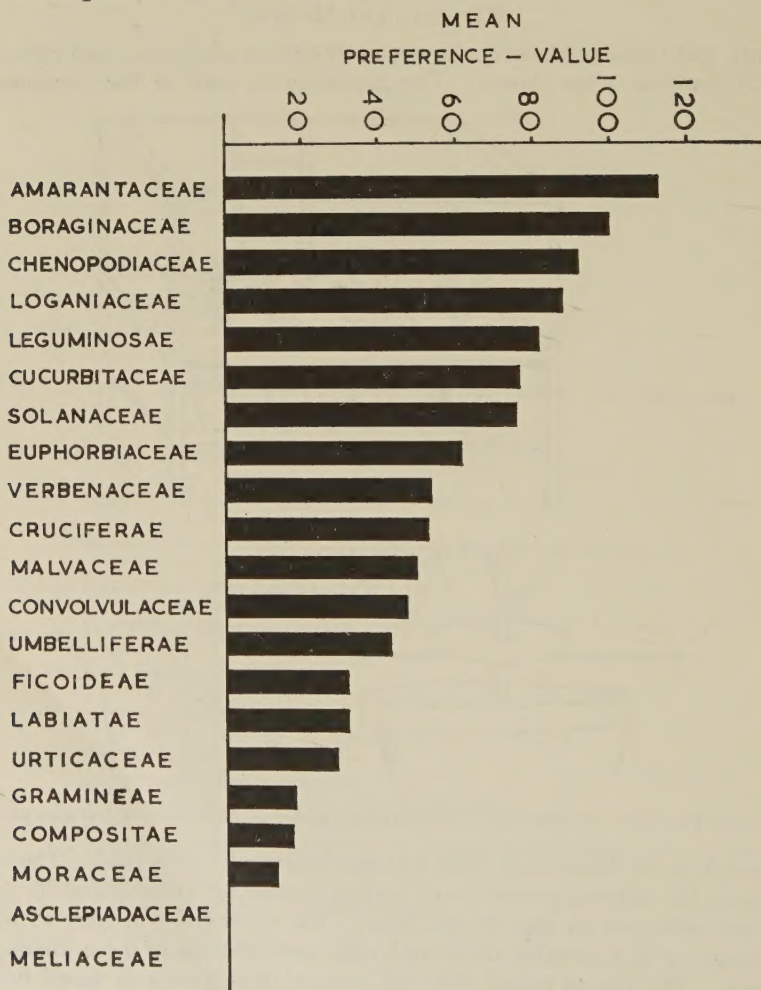

FIG. 2.—Mean order of preference of the different plant families.

RESULTS

The results of these experiments are summarised in Table I. Examination of the table shows that *Trifolium alexandrinum, Lycopersicum esculentum, Solanum tuberosum, S. melongena* and *Cucumis melo* var. *utilissima* are highly preferred amongst the cultivated plants. Of the 21 families (fig. 2) Amarantaceae, Chenopodiaceae, Loganiaceae, Leguminosae, Solanaceae, and Cucurbitaceae were the most preferred.

TABLE I.—*Order of preference of various plants*

| | Plant | Family | Order of preference | | | |
			Exp. 1	Exp. 2	Exp. 3	Mean
1.	*Heliotropium eichwaldi*	Boraginaceae	.	.	.	100
2.	*Solanum nigrum*	Solanaceae	92	50	49	64
3.	*S. melongena*	,,	55	123	97	92
4.	*S. tuberosum*	,,	98	113	107	106
5.	*Lycopersicum esculentum*	,,	121	124	111	119
6.	*Datura* sp.	,,	23	19	4	15
7.	*Capsicum annuum*	,,	50	74	.	62
8.	*Mentha viridis*	Labiatae	23	46	28	32
9.	*Saccharum officinarum*	Gramineae	8	10	11	10
10.	*S. spontaneum*	,,	0	0	0	0
11.	*Arundo donax*	,,	5	4	4	4
12.	*Pennisetum spicatum*	,,	23	21	.	22
13.	*Sorghum vulgare*	,,	33	50	77	53
14.	*Canabis sativa*	Urticaceae	30	25	31	29
15.	*Morus alba*	Moraceae	13	11	16	13
16.	*Amaranthus viridis*	Amarantaceae	88	81	171	113
17.	*Calotropis procera* (Flowers)	Asclepiadaceae	13	25	16	18
18.	*Calotropis procera* (Leaves)	,,	0	0	0	0
19.	*Azadirachta indica*	Meliaceae	0	0	0	0
20.	*Clerodendron inerme*	Verbenaceae	4	45	30	26
21.	*Lantana indica*	,,	93	71	.	82
22.	*Lagenaria vulgaris*	Cucurbitaceae	124	42	62	76
23.	*Momordica charantia*	,,	63	48	.	56
24.	*Cucurbita maxima*	,,	58	38	36	44
25.	*Cucumis melo* var. *utilissima*	,,	75	113	210	133
26.	*Daucus carota*	Umbelliferae	14	43	71	43
27	*Ipomea carnea*	Convolvulaceae	64	43	33	47
28.	*Trifolium alexandrinum*	Leguminosae	144	119	169	144
29.	*Dolichos biflorus*	,,	46	48	52	49
30.	*Acacia farnesiana*	,,	31	48	29	36
31.	*Cymopsis psoralioides*	,,	96	100	103	100
32.	*Euphorbia dracunculoides*	Euphoriaceae	103	69	103	92
33.	*Ricinus communis*	,,	32	29	.	31
34.	*Carthamus oxycantha* (Flowers)	Compositae	17	7	.	12
35.	*Carthamus oxycantha* (Leaves)	,,	0	0	0	0
36.	*Artemesia scoparia*	,,	26	46	28	33
37.	*Chenopodium album*	Chenopodiaceae	96	87	.	92
38.	*Buddleia asiatica*	Loganiaceae	73	108	83	88
39.	*Gossypium* sp.	Malvaceae	51	40	59	50
40.	*Trianthema monogyna*	Ficoideae	35	20	41	32
41.	*Raphanus raphanistrum*	Cruciferae	51	55	.	53

Saccharum spontaneum (Gramineae) and *Azadirachta indica* (Meliaceae) were totally rejected. In the case of *Calotropis procera* and *Carthamus oxycantha* the leaves were not attacked but the flowers were readily eaten.

Chrotogonus is known to cause serious damage to the seedlings of various cultivated plants, including even cereal crops and many forest trees (Ballard, 1914; Hargreaves, 1939; Beeson, 1941 and Kevan, 1954). The present investigations

show that mature plants of Gramineae are least preferred.   This can be attributed to the nature of the mandibles of *Chrotogonus* (Arora and Singh, 1958), which are best suited for feeding on tender forbs (Isely, 1944).   According to Maxwell-Darling (1934), *Chrotogonus* preferred *Euphorbia* (Euphorbiaceae) most of the seven plants tested ;   and *Panicum turgidum* (Gramineae), *Polygala triflora* (Polygalaceae) and *Tephrosia obcordata* (Leguminosae) were totally rejected.   *Chrotogonus* was, moreover, shown by Zacher (1917) and Golding (1948) to cause serious damage to mature tobacco plants.

Plants shown to be least preferred are nibbled at first, but eventually discarded, presumably because they are either hard to chew (e.g. *Saccharum spontaneum*) or have spiny leaves (e.g. *Carthamus oxycantha*—the leaves of which are readily eaten when the spines are removed), or are distasteful (e.g. *Azadirachta* and *Calotropis*).

Chrotogonus therefore feeds on young seedlings of plants irrespective of the preference shown for mature plants.   Its marked preference, on the other hand, for certain plants of economic importance belonging to the families Solanaceae, Leguminosae and Cucurbitaceae indicates that this insect may prove to be a serious pest even of mature plants.

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HYPOPHARYNGEAL GLAND DEVELOPMENT AND DIVISION OF LABOUR IN HONEY-BEE (*APIS MELLIFERA* L.) COLONIES

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Introduction

Hypopharyngeal glands retrogress in worker bees when the bees begin foraging (Soudek, 1927 ; Rösch, 1930) but may redevelop and secrete brood food again in response to the needs of their colony (Rösch, 1930 ; Moskovljevic, 1940). Probably, therefore, the occupation of a worker determines the condition of its hypopharyngeal glands to a considerable extent. In the present study the truth of the converse is investigated, *i.e.* whether the state of development of a bee's hypopharyngeal glands (as well as its previous experience) influence its occupation.

Methods and Results

There were seven similar experiments. Groups of newly emerged bees were marked and either released into a colony, or confined in it in cages which contained either (*a*) a comb of larvae, pollen and honey, or (*b*) a comb of pollen and honey only, or (*c*) an empty comb, in which sugar syrup was supplied in gravity feeders. After seven days (or, on one occasion, 14 days) the bees were released from the cages and a further group of newly emerged bees introduced into the colony. Observations were subsequently made for at least four hours daily at the hive entrance and marked bees which had been foraging (*i.e.* that were dusted with pollen, or had pollen in their corbiculae) were captured. A sample of ten bees from each cage had been retained when they were released. Their hypopharyngeal glands and those of captured foragers were classified into six arbitrarily defined stages of increasing development, stage 1 being totally undeveloped and stage 6 fully developed.

Table I.—*Mean ages (days) and S. E. of means when bees,*
subject to different treatments, began to forage
(Number of bees in brackets)

	Experiment				
	1	2	3	6	7
Free inside hive, beginning of week 1	23·0±0·62 (101)	24·5±0·22 (172)	21·1±0·21 (159)	21·0±0·29 (90)	17·1±0·95 (55)
Confined with sugar syrup during—					
Week 1			19·9±0·52 (34)	18·9±0·45 (17)	13·3±0·53 (33)
Weeks 1 and 2		26·4±0·63 (29)			
Confined with honey and pollen during week 1	29·3±0·71 (64)		21·0±0·38 (34)	21·1±0·80 (37)	15·5±1·01 (42)
Confined with honey, pollen and brood during week 1				19·2±0·21 (62)	16·3±0·84 (53)

The ages at which bees began to forage are given in Table I. On each of three occasions when bees were fed on sugar syrup for only one week, they subsequently began foraging significantly earlier than control bees of the same ages free inside

the hives ($P < 0.02$, $P < 0.01$ and $P < 0.01$ in experiments 3, 6 and 7 respectively), but bees fed on sugar syrup only for 14 days began foraging significantly later than control bees (experiment 2 : $P < 0.01$). Bees previously confined to combs containing brood, pollen and honey, or to combs containing pollen and honey only, began foraging at about the same time as control bees, and one group began later (experiment 1 : $P < 0.001$).

TABLE II.—*Mean stages of hypopharyngeal gland development of bees subject to different treatments.*
A : *on release of confined bees*　　B : *when they began to forage*

		Experiment						
		1	2	3	4	5	6	7
Free inside hive, beginning of	A.	3·90	3·61	3·86	.	.	4·55	5·00
week 1	B.	1·88	2·25	2·25	.	.	2·40	2·72
Confined with sugar syrup during—								
Week 1 . . .	A.	.	.	1·07	1·70	2·70	1·40	1·31
	B.	.	.	1·31	.	.	1·71	1·94
Weeks 1 and 2 . .	A.	.	1·00	.	.	.	.	.
	B.	.	1·74	.	.	.	.	.
Confined with honey and pollen during week 1	A.	3·58	.	2·18	3·20	4·20	4·00	3·00
	B.	1·91	.	1·77	.	.	2·70	2·68
Confined with honey, pollen and brood during week 1	A.	.	.	.	4·40	4·80	3·40	3·70
	B.	.	.	.	.	.	2·50	2·22

Table II shows the stages of development of the hypopharyngeal glands of bees subject to different treatments. When first released from their cages the hypopharyngeal glands of bees fed with sugar syrup were only slightly developed, presumably because of lack of pollen. The hypopharyngeal glands of bees confined in the other cages were considerably developed, but generally less so than those of the bees of the same age which had remained free inside the hive. (Bees confined with honey and pollen in experiments 3 and 7, $P < 0.01$ and $P < 0.001$ respectively ; bees confined with honey, pollen and brood in experiments 6 and 7, $P < 0.02$ and $P < 0.001$ respectively). This was probably because one set of cages contained no unsealed brood and the other set contained brood for only part of the time.

When bees began foraging the hypopharyngeal glands of the controls and those confined to combs containing brood, pollen, and honey, or combs of pollen and honey only, had retrogressed somewhat, whereas the glands of bees fed sugar syrup during confinement had developed a little, although they were still less developed than those of bees of the other groups. It seems unlikely, therefore, that the glands of the bees fed sugar syrup ever developed to the normal extent.

Observations in experiments 4 and 5 were eventually curtailed because the colony concerned became queenless and, eight days after the last bees had been released within it, part of the colony swarmed with a new queen. The swarm was hived and the marked bees in the swarm and parent colony counted (Table III). Relatively fewer of the bees confined during week 2 left with the swarm than did bees of the same age free inside the colony (bees confined with brood, pollen and honey − $P < 0.01$; bees confined with pollen and honey only −$P < 0.05$). The reason for this is unknown.

In each experiment, the colonies were examined when the confined bees were released and at three day intervals afterwards, and the distribution of the marked bees on brood and storage combs ascertained. The previously confined bees and the control bees of comparable age were distributed similarly (*see* Free, 1960).

Table III.—*Distribution of bees, subject to different treatments, in swarm and parent colony*

Treatment of bees	Age (days) of bees when colony swarmed	Number of bees	Number in swarm	% in swarm
Free inside hive, beginning of week 1 .	23	87	33	38
Confined with sugar syrup during week 1 .	23	28	10	36
Confined with pollen and honey during week 1	23	58	21	36
Confined with pollen, honey and brood during week 1	23	107	46	43
Free inside hive, beginning of week 2 .	16	103	63	61
Confined with sugar syrup during week 2 .	16	52	24	46
Confined with pollen and honey during week 2	16	35	10	28
Confined with pollen, honey and brood during week 2	16	125	47	38
Free inside hive, beginning of week 3 .	9	72	47	65

It was intended to carry out a further experiment to find whether foragers whose hypopharyngeal glands had redeveloped returned more readily to nursing duties than did those with undeveloped hypopharyngeal glands. However, three preliminary experiments in which captured foragers were confined in cages in the laboratory on a diet of either (*a*) sugar syrup and water, or (*b*) pollen-candy mixture and water, or of (*c*) pollen-candy mixture and water with, in addition, young larvae to feed, showed that only with the last did the hypopharyngeal glands redevelop to any extent (Table IV); the use of foragers which had been reconditioned to feeding larvae would, of course, have defeated the object of the intended experiment.

Table IV.—*The redevelopment of the hypopharyngeal glands of foragers*

Experiment	Date of capture		Dissected immediately after capture	Confined in cage for 7 days with :		
				Sugar syrup and water	Pollen-candy mixture and water	Pollen-candy mixture, water and larvae
1	13th May	Number of bees	31	40	38	33
		Mean stage of hypopharyngeal gland development	2·80	1·70	1·87	3·52
		% bees with developed hypopharyngeal glands (Stages 4, 5 and 6)	25·8	2·5	5·3	54·5
2	15th July	Number of bees	33	52	46	66
		Mean stage of hypopharyngeal gland development	1·90	1·90	2·01	2·58
		% bees with developed hypopharyngeal glands (Stages 4, 5 and 6)	3·0	7·7	6·5	27·3
3	5th August	Number of bees	30	46	38	.
		Mean stage of hypopharyngeal gland development	2·07	1·33	1·82	.
		% bees with developed hypopharyngeal glands (Stages 4, 5 and 6)	0	0	7·9	.

DISCUSSION AND CONCLUSIONS

It is doubtful whether the bees kept solely on carbohydrates ever had hypopharyngeal glands sufficiently developed to feed brood, and they probably foraged earlier than the control bees because they omitted nursing duties. Bees kept on a carbohydrate diet until 10 days old can still develop their hypopharyngeal glands when fed protein (Kratky, 1931), so that the stage of development of these glands can probably determine the occupation to some extent.

Lindauer (1953) and Butler (1954) suggested that lack of work inside the hive may induce household bees to become foragers. However, bees confined on a carbohydrate diet, or a protein diet without larvae being present, did not forage soon after their release, so this suggestion can only be generally applicable when bees are approaching normal foraging age or when they have done hive duty for a minimum period first. Because bees confined to a carbohydrate diet for two weeks began foraging later than control bees, the latter alternative seems the more probable.

The hypopharyngeal glands of foragers can redevelop and enable them to feed brood should their colony need it. The present evidence suggests that foragers, and possibly young bees also, need to be stimulated by the presence of larvae for their glands to develop to the maximum and that a protein diet alone is insufficient.

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THE BEHAVIOUR OF TSETSE FLIES
(*GLOSSINA SWYNNERTONI* AUSTEN)
IN RELATION TO PROBLEMS OF SAMPLING

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INTRODUCTION

STUDIES of tsetse populations by methods of marking, release and recapture (Jackson, 1933, 1948) have made it possible to predict, admittedly only within fairly wide limits, what an unbiased sample of a tsetse population should comprise in terms of males and females and of flies in the different stages of the hunger cycle. There is a glaring discrepancy between this expectation and the composition of samples obtained by current methods of collection such as fly-round catches (*e.g.* Jackson, 1930), resting catches (Isherwood, 1957), catches on bait animals and in traps (Jack, 1941); and the results are not such that a representative sample could be expected from the use of a combination of methods.

The fact that current sampling methods introduce a serious bias need not, however, preclude critical interpretation of the results, provided the investigation can be shown to be independent of such bias (as in much of Jackson's population work, *e.g.* 1948) or provided the nature and degree of bias can be evaluated. This latter problem has unfortunately not received the attention it deserves.

The most widely used method for sampling tsetse populations is based on the propensity of certain sections of the population to approach or attack a moving party of men. The catches made are strongly biased in many ways, some of which have long been recognised; for instance, they include only a very small fraction of the female population, and most of the males caught are in the later stages of the hunger cycle. The explanation usually put forward to account for this type of bias is that, while females come to the catching party only to feed, and hence only in the last stage of the hunger cycle, males come in part to mate and in part to feed, so that only the very early stages of the hunger cycle fail to be adequately represented (this interpretation is discussed in some detail by Swynnerton, 1936 : 83; and by Buxton, 1955 : 184). According to this view the flies which follow a catching party should give a reasonable sample of the hungrier elements of the male population; but the experiment reported below, undertaken to determine at what stage of the hunger cycle tsetse flies become ready to feed, gave results which did not agree with this expectation.

MATERIAL AND METHODS

Collections of *Glossina swynnertoni* were made in Block 9, a 50 square mile remnant of tsetse habitat near Shinyanga, Tanganyika, during February and March, 1959; samples were taken between 07.00 and 12.00 hours and four different methods of sampling were used in an attempt to distinguish potential feeders from non-feeders :

(*a*) flies caught approaching or attacking a catching party consisting of the author and two African assistants ;

(*b*) flies caught while attempting to probe the skin of a young heifer recumbent in the shade of a clump of tress (with three catchers) ;

(*c*) flies caught at their perching places on trees, the approaching or attacking flies of sample (*a*) having been caught out as far as possible (Isherwood, 1957);

(*d*) flies attracted to a slow-moving lorry, stops being made for catching every 500 yards.

In this paper, these samples will be referred to as the standard, the bait, the resting and the vehicle catch respectively.

Flies were killed with potassium cyanide immediately on capture and transferred to glass-stoppered tubes lined with moist filter paper for transport to the laboratory. The procedure for determining size (thoracic surface), water content, fat content and residual dry weight have been described elsewhere (Bursell, 1959*a*, 1960).

Male flies may be assigned to different stages of the hunger cycle on the basis of their external appearance, four categories being currently recognised, namely, gorged (stage I), replete (stage II), intermediate (stage III) and hungry (stage IV) (*see* Jackson, 1933). The criteria used for the identification of the different stages are based in part on the amount of residual blood meal left in the gut, and in part on the degree of development of the abdominal fat body. It seemed desirable for present purposes to separate these two aspects of nutritional state in view of the possibility that they may not at all times be closely dependent. The amount of undigested blood remaining in the alimentary canal cannot easily be determined directly, but approximate estimates were obtained by comparison with flies starved to death at high humidities on the assumption that in such flies none of the blood meal remains. The relation between thoracic surface (X, in arbitrary units) and the residual (non-fatty) dry weight of the abdomen (Y, in mg.) was determined as

$$\hat{Y} = 0.179X - 0.262$$

so that, given the size, an estimate of the starved abdominal weight of any fly could be obtained. The difference between this and the recorded residual dry weight of the abdomen has been taken to represent the weight of the residual blood meal. Estimates made in this way would be subject to considerable error if non-fatty food reserves occur outside the gut, but this is a possibility which cannot at present be allowed for. The amount of residual blood meal is expressed as a percentage of the full meal calculated on the basis of a previously determined relation between the thoracic surface (X) and the weight (Y, in mg.) of blood taken by non-teneral flies at a full feed, taking the water content of blood as 78.9 per cent. (*see* Jack, 1939); this relation is given by the formula

$$\hat{Y} = 9.38X - 40.6$$

For critical comparison it was necessary to make a correction for differences in size; this was done by calculating the appropriate regression and comparing the samples at a specified level of the independent variate. Values obtained in this way will, in what follows, be referred to as " specific " to the independent variate, *e.g.* " size-specific " or " *RBM*-specific ".

The second criterion used in hunger diagnosis (the degree of development of the abdominal fat body) is reflected in the fat content of the fly as a whole, since most of the reserves are deposited in the abdomen. For critical comparison it was necessary to make a correction for differences in size; this was done by calculation of the appropriate regressions to give size-specific values.

The water content of the thorax was determined as a measure of tissue hydration, but since no differences could be established between the different samples the results have not been included.

In females the situation is complicated by the developmental cycle of the larva in the uterus and the presence in the abdomen of the milk glands which have substantial amounts of lipoid reserve (Hoffmann, 1954); for these reasons analyses have

been confined to non-pregnant individuals and the fat content of the thorax only has been taken as giving an indication of the extent of the reserves. Also, since females containing appreciable amounts of blood occur only in the resting catch, these also have been excluded, and results refer to " hungry " females only. The regression of the fat contents against thoracic residual dry weight was calculated, and comparisons made at specified levels of this measure of size.

RESULTS

Figure 1 (I) *a–d* shows the frequency distributions of percentage residual blood meal (*RBM*%), and the relation between *RBM* percentage and fat content for the four samples. The resting catch is characterised by a high proportion of flies with more than 30 per cent. *RBM*, a category which is represented in none of the other samples ; a second peak occurs between 4 and 10 per cent. *RBM*, but values above 10 per cent. are common, and a few flies were taken with very low *RBM* values. The standard catch is characterised by a strong mode between 4 and 8 *RBM* percentage, with few flies below the mode and a well-developed tail above it. The vehicle catch is similar except for an increase in frequencies below the mode and a decrease above. The bait catch is distinguished from all the others by a strong preponderance of flies in the lowest *RBM* categories.

In general terms it may be said that flies in both the very early and the very late stages of the hunger cycle escape capture by methods which involve an attraction of the flies to moving objects.

Although the catches made by the four different methods can be distinguished on the basis of these frequency distributions, there is substantial overlap between the curves, the 4–8 per cent. *RBM* categories, in particular, being well represented in all. But consideration of the fat contents of flies at this stage of digestion (shown in fig. 1 (II)) makes it clear that, although they have reached the same stage of digestion, they are by no means equivalent in respect of nutritional state. The

TABLE I.—*The fat content of males with a residual blood meal percentage between 4 and 8 sampled by different methods, and the percentage of females caught*

			Method of collection			
					Simultaneous catches	
	Resting catch	Standard catch	Vehicle catch	Bait catch	Standard catch	Bait catch
N	12	25	23	25	17	9
Thoracic surface ($\bar{x}_1$)	$8\cdot10\pm0\cdot08$	$7\cdot82\pm0\cdot08$	$7\cdot80\pm0\cdot08$	$7\cdot53\pm0\cdot08$	$8\cdot04\pm0\cdot11$	$7\cdot91\pm0\cdot14$
RBM % ($\bar{x}_2$)	$5\cdot80$	$6\cdot08$	$5\cdot84$	$5\cdot88$	$5\cdot75$	$5\cdot17$
$b_{y1\cdot2}$	$1\cdot028$	$0\cdot931$	$1\cdot493$	$1\cdot099$	$1\cdot101$	$0\cdot645$
$b_{y2\cdot1}$	$0\cdot254$	$0\cdot110$	$0\cdot302$	$0\cdot230$	$0\cdot466$	$0\cdot246$
$s_{y0\cdot12}{}^2$	$0\cdot204$	$0\cdot448$	$0\cdot536$	$0\cdot460$	$0\cdot474$	$0\cdot594$
R^2	$0\cdot52$	$0\cdot23$	$0\cdot40$	$0\cdot31$	$0\cdot35$	$0\cdot19$
		(*Size* $= 7\cdot80$; *RBM* $= 6\cdot0$%)			(*Size* $= 8\cdot0$; *RBM* $= 5\cdot5$%)	
Specific fat contents	$2\cdot34\pm0\cdot19$	$3\cdot16\pm0\cdot14$	$2\cdot68\pm0\cdot15$	$2\cdot39\pm0\cdot17$	$2\cdot58\pm0\cdot11$	$1\cdot98\pm0\cdot22$
% *N-T* females	21	4	18	50	5	47

Thoracic surface (X_1) is given in arbitrary units, fat content in mg.

$b_{y1\cdot2}$ and $b_{y2\cdot1}$ are the coefficients of regression of fat on thoracic surface and *RBM* percentage respectively.

$s_{y0\cdot12}{}^2$ is the mean square of fat content when $X_1 = \bar{x}_1$ and $X_2 = \bar{x}_2$.

R^2 represents the proportion of the total variance to be attributed to the regression.

N-T = non-teneral ; the percentages of non-teneral females in the total non-teneral catch are based on large samples ($N > 100$), except for the simultaneous catches for which the numbers in the samples were 38 on the bait and 41 on the standard party.

flies of the standard catch have the highest fat content, and the flies caught on the bait animal the lowest, the amount of overlap between the two being extremely slight ; the distribution in the vehicle catch differs from that in the others in being much flatter, and its general form is such as would result from a combination of standard and bait catches ; the fat contents of the resting catch are somewhat smaller than those of the standard catch, but not as low as for the bait catch.
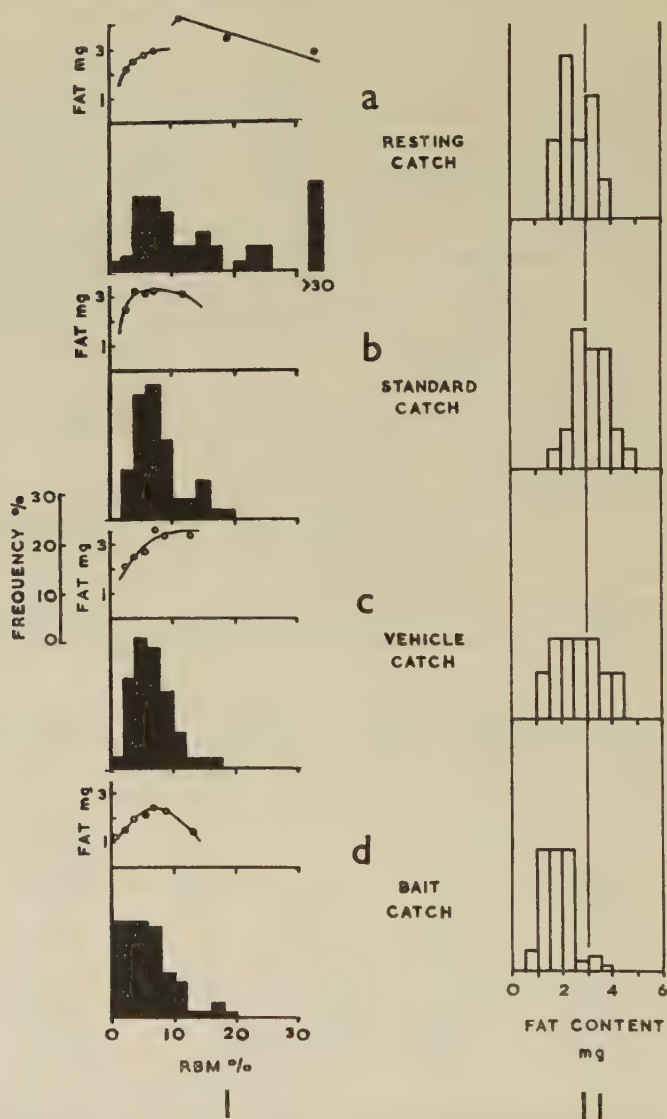

Fig. 1.—The nutritional state of male tsetse flies sampled by different methods.

I. The frequency distribution of percentage residual blood meal (*lower*) and the fat content at different stages of digestion (*upper*).

II. The frequency distribution of fat contents for flies at late stage of digestion (*RBM* percentage between 4 and 8) ; analysis of the resting catch was based on 40 flies, of the standard catch on 48, of the vehicle catch on 46, and of the bait catch on 68.

For comparison with standard methods of hunger staging the residual blood meal percentage of "classical" hunger stages have been determined as follows :
Stage I, 50 per cent. *RBM* ; II, 20 per cent *RBM* ; III, 8 per cent. *RBM* ; IV, 3 per cent. *RBM*.

The detailed comparison between these catches is, however, complicated by yet another kind of sampling error, which is reflected in differences in the mean size of the flies collected (*see* Table I, line 2). The flies of the resting catch are significantly larger than those of the standard and vehicle catches, and the latter in turn are larger than the bait catch. The reason for these differences becomes clear when it is realised, in the first place, that the months preceding the present collections were characterised by a marked increase in the mean size of flies (*see* Glasgow and Bursell, 1960); and secondly, that there is a tendency for flies to be inactive, or rather, reluctant to appear to catching parties, during their early life (Jackson, 1946); young, and hence large, flies will therefore predominate in the resting catch as compared with the standard and vehicle catches. With regard to the bait catch, this differs from the two latter catches, not only in regard to the nature of the attracting stimulus, but in being a stationary catch; in other words, the flies have to enter the zone of attraction by their own activity, while with the other types of catch the attracting stimuli are, as it were, brought to the flies. This means that in the sample collected from the bait animals there will be an even greater proportion of active, older, and therefore smaller, flies, than in the moving catches.

These differences in mean size can, however, be allowed for by a more detailed analysis of flies with an *RBM* between 4 and 8 per cent. which are well represented in all catches. Reference to figure 1 (I) shows that there is, over this range of *RBM*'s, a strong relation between fat content and *RBM*, so that it was necessary to calculate multiple regressions, taking *RBM* and size as the independent variables. The results of this analysis are set out in Table I, columns 1–4, the size- and *RBM*-specific fat contents being given in line 8. The data confirm some of the conclusions reached by inspection of the frequency distributions, namely that the fat content of the standard catch is significantly larger than that of the vehicle catch, which in turn is larger than that of the bait catch. But, clearly, the comparatively high fat content of the resting catch must be attributed entirely to the greater size of these flies, for corrected values show no difference between resting and bait samples.

The interpretation put forward to account for the differences in mean size has been confirmed by analysis of the distribution of wing fray categories (Jackson, 1946); these showed that the percentage of early categories (1 and 2) was 45 in the resting catch, 30 and 34 in the standard and vehicle catches and only 18 in the bait catch.[1] This difference in age raises a further doubt concerning the comparison between stationary and moving catches, because it is known that older flies tend to be deficient in fat (*unpublished data*). In order to settle this doubt two further samples were collected, the data for which have been included in Table I (columns 6 and 7); here a standard catching party walked continuously round the bait party at a distance of about 25 yards. For both samples, therefore, flies had to enter the zone of attraction, and the collection showed correspondingly few flies in the early wing-fray categories (12 out of 55 = 22 per cent.). These catches were made about a month after the ones discussed above, which accounts for the rather greater mean size of the flies; but, unlike the earlier catches, they show no significant difference in size. The fat content of the bait catch is about 0·6 mg. less than that of the standard catch, a difference slightly smaller than that previously recorded, but still statistically significant.

Some data for females, distinguished as " hungry " on the basis of external appearance, are given in Table II. The situation differs markedly from that described in males, for the fat content of the standard catch is lowest, that of the resting and vehicle catches highest, the bait catch being intermediate. There are also some striking differences in variability—in the standard catch all the flies have low fat contents and in the vehicle catch all have high, while in the resting and bait catches

[1] The difference between these three levels has been tested with Chi square and found to be significant at the 5 per cent. level (*N* is between 90 and 105 for each of the samples).

some have low and some high. These differences in variance have been examined on the basis of the distribution of z (Fisher, 1936 : 230) and found to be statistically significant (z for the vehicle/resting catch comparison is 0·62 ($P = 0.05$–0.01) and for the bait/standard catch comparison 0·72 ($P < 0.01$)).

The results in general suggest that there is a very marked difference between flies attracted to moving objects and to stationary bait animals ; ideally one might imagine that a tsetse in a given physiological state would either be attracted to a moving party and not to the bait, or it would be attracted to the bait and not to the moving party. If this independence were absolute, catches by the two methods should be unaltered even if the stimuli were presented simultaneously. In practice this test of independence is not an easy one to apply, because the number of flies taken by either means varies considerably from time to time and from place to place. But the problem may be approached with reference to the proportion of females caught. It has already been mentioned that the percentage of females taken by a

TABLE II.—*The size-specific fat contents of the thorax in females sampled by different methods*

	Method of Collection			
	Resting catch	Vehicle catch	Bait catch	Standard catch
N	12	13	10	16
Thoracic RDW ($\bar{x}$) . . .	6·83	6·70	6·79	6·82
b	0·147	0·201	0·056	0·119
$s_{y·x}^2$	0·0214	0·0064	0·0435	0·0104
Size-specific fat content				
$RDW = 6·80$ . . .	0·772$\pm$0·042	0·770$\pm$0·022	0·675$\pm$0·066	0·520$\pm$0·026

RDW = residual dry weight ; b = regression coefficient and $s_{y·x}^2$ = mean square when $X = \bar{x}$.

standard catching party is very low ; the bait sample on the other hand gives a sex ratio of about 1 : 1 (*see* Table I). Clearly if the two attractant stimuli are presented simultaneously, and if the samples are not independent, then some of the males which would otherwise have been attracted to the bait will be intercepted by the catching party, with the result that the female percentage of the bait catch should increase. In fact the results obtained with the simultaneous catches described above give no indication of an increase in the percentage of females at the bait animal (see 4th and 6th figures in last line of Table I), and it may be concluded that the males caught by the standard party would not have been attracted to the bait, in other words that the two samples are, within the limits of error of the method, independent.

THE HUNGER CYCLE

On the basis of these results, and of earlier, published work, it is possible to visualise, in very tentative terms, the cycle of events which make up a hunger cycle. It will be convenient for this purpose to divide the hunger cycle of the male tsetse fly into four main phases :

Phase 1

The first phase is characterised by almost complete inactivity (Bursell, 1957) and comprises the period during which the blood meal is concentrated by excretion of water (Jackson, 1933 ; Jack, 1939), the rate of digestion being high and the products of digestion rapidly converted to fat (Jack, 1939 ; Mellanby, 1936). At this time flies are unresponsive to the stimuli provided by moving objects or by bait animals, so that they can only be sampled at their perching places.

Phase 2

After the partial digestion of the blood meal and replenishment of fat stores, flies enter upon the active phases of the hunger cycle. In the laboratory spontaneous activity has been found to increase progressively (Bursell, 1957), and evidence in connection with the rate of utilisation of fat suggests that this applies also under natural conditions (*unpublished data*). The movement of flies in the absence of more specific stimuli is probably related to particular features of the vegetation, which will tend to restrict dispersal and confine the flies to recognisable " ambits " (Jackson, 1944). The function of this movement is perhaps to increase the frequency of mating and host encounter. Of the flies which meet a moving object in the course of this phase of the hunger cycle, those which have relatively abundant fat reserves will approach and follow this object, and the response may be regarded as a kind of sexual appetitive behaviour. The occurrence of this behaviour pattern implies the absence of such flies from the resting catch, for they will be attracted to the party which comes to inspect the perching sites, and will be included in the standard catch (see *Methods*). This separation of the two phases is reflected in the discontinuous relation between *RBM* percentage and fat content illustrated in figure 1 (I) *a* ; the resting catch includes, on the one hand, flies which are still in the process of accumulating fat reserves and have not yet become active, and on the other, flies whose fat reserves have become so depleted that they have ceased to be responsive to the presence of a catching party (*see below*). The implication is that the duration of that phase of the hunger cycle characterised by attraction to moving objects is a limited one, and of this there is evidence of quite a different kind ; for it is common experience that in walking through a tsetse habitat the size of the " following swarm " (Swynnerton, 1936) does not increase indefinitely. In view of the results illustrated in figure 1, it is not unreasonable to suppose that waning of the sexual appetitive response is linked to the concurrent depletion of food reserves, the rate of which is of course enormously increased during the continuous flight which characterises the following swarm (*see* Bursell, 1959*b*) ; in other words, that when reserves fall to a certain level flies cease to follow, being replaced continuously by newly encountered individuals.

The very low fat content of flies taken on the bait animal in relatively early stages of digestion (*RBM* over 12 per cent., *see* fig. 1 (I) *d*) suggests that phase 2 may not be an obligatory component of the hunger cycle. It seems likely that the fat reserves of some flies may become so depleted that a single blood meal does not suffice to replenish them to the level characteristic of phase 2 flies. After the inactive phase of the hunger cycle these would enter straight upon phase 3.

Phase 3

The waning of the response to moving objects may be said to end the second phase of the hunger cycle ; activity continues at a high level but the response towards which the activity may be regarded as directed is different, being now the first link in the chain of reactions which leads to the processes of probing and feeding. Flies in this phase are characterised by low *RBM* percentage, low fat content and indifference to moving objects, and they therefore occur neither in standard catches nor in vehicle catches. They are well represented in the resting catch, and it is clear that the term " resting catch " or " resting flies " here and elsewhere in the literature (*e.g.* Nash, 1952 ; Glasgow *et al*., 1958) implies nothing more than that the flies are unresponsive to the stimulus of moving objects ; of such flies those which are in the early phase of the hunger cycle may perhaps be said to be truly resting, but there is no evidence that the level of activity of other " resting " flies is any different from that of flies caught by different means.

Flies in phase 3 are attracted to potential hosts and make up most of the bait catch; but that a stimulus situation adequate for the release of the feeding reaction is not often encountered is indicated by the accumulation of flies with low percentages of residual blood meal at the bait animal (*see* fig. 1 (I) *d*). The mean fat content of flies with less than 1 per cent. *RBM*, which make up 12 per cent. of this sample, is 0·8 mg.; with the critical fat content at about 0·5 mg., they have an average of less than six hours left to live (*from unpublished data*).

Phase 4

It should be mentioned that the present work was done during the rainy season, at which time the level of nutrition is at its highest (Glasgow and Bursell, 1960). Standard collections made at other times of the year show a greater proportion of flies with low *RBM* values and fat contents. The results of these collections will be published elsewhere, but here it is relevant to note that there is a tendency for the frequency distribution of fat-contents to show a secondary peak near the lethal limit, and it is suggested that there may be a fourth phase of the hunger cycle, characteristic of flies in a state of inanition, during which a moving object becomes an adequate stimulus for the release of the feeding reaction, and that such flies will be well represented in a standard sample.

With regard to the female tsetse fly, our knowledge is hopelessly inadequate; but it would seem reasonable to suppose that the general sequence of events during the hunger cycle may be similar to that suggested for males, except for the complete absence of phase 2, the phase of activity associated with sexual appetitive behaviour. The absence of this active phase would be in accord with the fact that the wings of females fray much more slowly than those of males; and might also in some measure account for their longer mean life—they would be less exposed to the attack of predators such as asilids and dragonflies, and, since food reserves would be expended less quickly, in less danger of death by starvation. The invariably low fat content of females attracted to standard catching parties lends some support to the idea of a final phase of the hunger cycle during which the threshold for the feeding reaction is lowered to a level where a catching party becomes an adequate stimulus. The bait catch would include some females which, for lack of earlier host encounter, have low fat reserves and others still in early phase 3, hence the somewhat higher mean fat content of the catch as a whole, and the very high level of variability. In the resting catch, phase 4 females would not be represented at all, hence the still higher and less variable fat content characteristic of this sample.

The vehicle catch remains to be considered; this method of sampling is generally eschewed on the grounds that it produces an abnormally " hungry " sample of the population, as judged by the proportion of stage IV males and of females (Jackson, 1937; this view has been questioned by Jack (1939)). Present results have shown that male flies attracted to a vehicle tend to be in a slightly later stage of digestion and that their fat content at a given stage of digestion is lower than that of flies caught by the standard method; and that females are caught in relatively greater numbers. These differences could be accounted for, in terms of the suggestions made above, on the further assumption that considerations of size enter into the reaction to moving objects as potential hosts; in other words, that at a given reaction threshold a response may occur to large objects while smaller objects would fail to elicit the following reaction. On this view the catch on a vehicle would be expected to comprise males in phase 2 (the phase of sexual appetitive behaviour), males and females in phase 4 (the phase of inanition) and that fraction of the males and females in phase 3 whose reaction threshold, too high to permit of a response to normal catching parties, is yet low enough to enable a response to a more intense stimulus; the composition of the sample, intermediate between the standard and the bait catch, in respect of male *RBM* percentage and fat content and female percentage,

is in accord with this interpretation. It would appear, then, that a vehicle catch provides the more comprehensive sample of a population, and it is rather the standard catch which should be viewed with suspicion, as giving an abnormally replete sample.

DISCUSSION

One of the main difficulties about accepting the concept of male following as a form of sexual appetitive behaviour is that so few females are attracted to the same object. This anomaly is emphasised by the present results, since only a very small fraction of the following swarm will feed, so that mating must figure as the sole object of their following ; it would be resolved if the following activity of males is a mechanism for ensuring the fertilisation more specifically of *teneral* females, that is, of females which have lately emerged from their pupae and have not yet had their first blood meal. The selective advantage of *early* fertilisation cannot be doubted for a genus whose reproductive potential can be so greatly affected by the difference of a day in the time at which embryonic development starts (which may make the difference between, say, four pupae and three, or between one pupa and none) ; and there is abundant evidence that early fertilisation is, in fact, achieved under natural conditions. Vanderplank (1947) for example, reports the dissection of 10,000 *G. swynnertoni* of which *all* the non-teneral females were found to be inseminated, while about two-thirds of the teneral females had not yet mated.

If this interpretation of the male following is correct, it implies that moving objects, such as a catching party, constitute for teneral flies an effective stimulus to feed. That this may indeed be so is suggested by the observation that teneral flies regularly attempt to feed off catching parties, and above all by the fact that samples of teneral flies obtained on fly rounds are unbiased with respect to the proportion of the sexes, the ratio being usually close to unity (*e.g.* Jackson, 1944).

Some previously published data on the composition of teneral *G. morsitans* Westw. (Bursell, 1959*a*) are relevant in this connection. They show that the fat content of both sexes is lower in flies attracted to a catching party than in those which remain to be caught off the vegetation. Thus the situation resembles that obtaining for non-teneral females and for non-tenerals of both sexes in phase 4 of the hunger cycle, in all of which the attraction to moving objects may be regarded as a reaction to potential hosts. It might in fact be permissible to regard tenerals as belonging automatically to phase 4 ; the mean fat content of tenerals of *G. swynnertoni* on the day after emergence is given as 1·09 mg. (Bursell, 1959*a* : Table V) and comparison with values shown in figure 1 of the present paper show that this would correspond to a very late stage of the non-teneral hunger cycle.

One of the most striking features of the present results lies in the distinction which may be drawn between stimuli which will evoke sexual appetitive behaviour and those which will give rise to the feeding reaction. Exactly what are the effective differences between the two stimulus situations presented, whether the presence of a bait animal, the absence of movement or the shady situation, has not been determined. There is evidence that shade may be a factor of importance in eliciting the feeding response (F. Isherwood and H. A. W. Southon, *personal communication*) ; and if the attraction of a higher proportion of females may be taken as a criterion of the stimulus to feed, there is evidence in the literature that quiescence may also be of great importance ; for it is known that standing catches give a considerably higher female percentage than moving catches (Jack, 1941), while, on the other hand, the presence of bait animals in a moving catch has a somewhat unpredictable effect—they often increase the female percentage but these seldom approach the high levels characteristic of the present bait catch (*e.g.* Nash, 1933 ; Jackson, 1930). It is particularly noteworthy that, although over 70 per cent. of the blood meals collected from the area in which the present investigation was carried out have been identified as warthog (Glasgow

et al., 1958) the presence of warthog in a moving catch had no effect on the female percentage (Johns, 1958).

The possibility that quiescence and shade may be important components of stimulus situations which elicit the feeding reaction may go some way towards resolving the striking discrepancy between the apparent availability of different species of potential hosts in a tsetse habitat, and the frequency with which they are fed on by the tsetse fly (Weitz and Jackson, 1955 ; Weitz and Glasgow, 1956 ; Glasgow *et al.*, 1958). For on this view the factor which would make for " preference " would be a tendency of hosts to lie up in shady situations during most of the day. If the categories of Weitz and Glasgow (1956) are examined in this light, the correspondence is reasonably close. For, of the animals commonly or " always " bitten, a high proportion (8 out of 12) are known to spend a great part of their day lying up under shade (warthog, rhinoceros, man, reedbuck, buffalo, kudu, bushpig and bushbuck) ; while for the majority (10 out of 15) of those rarely or " never " bitten, this would not apply (eland, duiker, impala, baboon, monkey, birds, hartebeest, topi, zebra and wildebeest). The exceptions in the second group include such as would often lie up in places not frequented by tsetse fly (hyaena and porcupine), while the occurrence of elephant and giraffe as exceptions in the first group could, on the basis of the interpretation of vehicle catches, be referred to some extent to their large size. The advantage of feeding on resting animals cannot be doubted in view of the vigorous reactions of many species to the attack of biting flies (Harrison, 1940)—reactions which in the case of the bait animal used for the present series were observed to cause the death of feeding flies on several occasions. It is not suggested that the feeding of tsetse flies in a given situation can be explained in any simple terms ; a complex of factors, of which the density of potential hosts and the degree of overlap between the " ambits " of the tsetse and the distribution of hosts will be important, must be invoked to account for any particular feeding incidence. But it is unlikely that much progress will be made in the interpretation of available results until more is known of the details of the behaviour of host animals.

The results of the present investigation have shown that standard methods of sampling do not provide a representative sample of flies in the later stages of the hunger cycle ; for the catch includes predominantly those individuals which have reached a late stage in digestion without serious depletion of their fat reserves. This deficiency in the sampling method must be borne in mind in assessing the implications of results obtained by it, and some of the standard concepts in tsetse biology, such as apparent density, availability and mean hunger stage (*see* Buxton, 1955) will require re-examination.

Finally, I wish to thank Professor D. W. Ewer and Dr. R. F. Ewer for reading the manuscript and suggesting various improvements.

SUMMARY

1. The fat content and residual blood meal of flies sampled in four different ways (standard catching party, resting catch, catch from bait animal, and from vehicle) were determined.

2. The fat content of flies in a late stage of digestion was high for the standard catch, low for the resting and bait catches and intermediate for the vehicle catch. The proportion of females caught showed the opposite trend, being low in the standard catch, high in the resting and bait catches and intermediate in the vehicle catch.

3. These findings were interpreted in terms of changes in the behaviour of flies in the course of the hunger cycle. Four phases were recognised in the male hunger cycle :

(1) Phase of inactivity.

(2) Phase of activity characterised by sexual appetitive behaviour.

(3) Phase of activity characterised by appetitive behaviour in relation to the feeding reaction, but by indifference to the stimulus of moving objects.

(4) As for (3) except that moving objects here constitute an adequate stimulus for release of the feeding reaction.

4. The bearing of these results on the problem of " host preference " is discussed.

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FURTHER STUDIES ON THE GROWTH STAGES OF *ARIXENIA ESAU* JORDAN AND *ARIXENIA JACOBSONI* BURR (DERMAPTERA: ARIXENIIDAE), WITH A NOTE ON THE FIRST INSTAR ANTENNAE OF *HEMIMERUS TALPOIDES* WALKER (DERMAPTERA: HEMIMERIDAE).

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INTRODUCTION

THE Dermaptera *Arixenia esau* Jordan, 1909 and *Arixenia jacobsoni* Burr, 1912 are widely known to be associated with bats of the Indo-Malayan region. Several recent papers (Cloudsley-Thompson, 1957, 1959; Medway, 1958) have dealt with various aspects of the biology of one or both of these species. That of Medway is concerned with the habits of *A. esau* in the Niah Caves, Sarawak. In the earlier paper, Cloudsley-Thompson deals with a large collection taken from a hollow tree in Selangor, Malaya and is mainly concerned with the growth stages of both species. In his later paper he discusses some points made in the first and suggests that certain of them might well be amended.

The present paper is concerned mainly with the first instar of both species of *Arixenia* and also discusses some of the points made by Cloudsley-Thompson (1957, 1959).

It has been shown by several authors that in the true earwigs (Forficulina) moulting is accompanied by an increase in the width of the head capsule and in the number of antennal annuli (*see* Table I). *Arixenia* has invariably been grouped with the Forficulina, sometimes at the family level—Jordan (1909), Deoras (1941) and Handlirsch (1925, 1926, 1939), but generally by later authors at the subordinal level—Burr (1911), Burr and Jordan (1913), Tillyard (1926), Chopard (1949) and Imms (1957). The latter course will be followed here. The writer has, however, shown (Giles, 1955) that the Arixeniina and the Forficulina have very close morphological relationships and it is therefore assumed here that the condition of the antennae in the first instar and during development and of the composition of the regions (Giles, 1952) is the same in the two suborders.

Cloudsley-Thompson's paper (1957) has already been mentioned, but a comparison between the data in his Table I and item 3 of the summary seems desirable. The growth ratio is not nearly constant in *A. jacobsoni* from Java, and, in fact, it would seem that an instar could have been missed before the fourth and that there is a decrease in size between the fifth and the adult male. The small numbers under consideration might account for these anomalies. In three other places the growth ratios are well away from the trend of the respective species. The overlapping of head widths of successive instars of *A. esau* (the one species where reasonable numbers are available) is considerable—76 instances in 185 specimens. Although the majority do not overlap, it is evident that head width is not a reasonably accurate guide for instar determination. However, the numbers of antennal annuli do provide a reliable means of separating instars in all the species listed in Table I. This point is made on p. 6 of Cloudsley-Thompson's paper.

In Cloudsley-Thompson's Table I and figure 2, the meriston is not considered to be part of the middle region of the antenna (Giles, 1952). There seems to be no reason to depart from the writer's original arrangement whereby the meriston and all annuli produced by it form the middle region of the antenna.

THE FIRST INSTAR OF *Arixenia*

In his earlier paper Cloudsley-Thompson (1957) considers that both *A. esau* and *A. jacobsoni* pass through five nymphal instars during development. However, in his later paper (1959), after considering evidence afforded by embryos from two females of *A. esau* from the Niah Caves, he concludes that each species " probably had four nymphal instars ". It will be demonstrated here that both *A. esau* and *A. jacobsoni* do have but four nymphal instars.

Embryonic Condition

Cloudsley-Thompson (1957) thought it probable that the two species of *Arixenia* are ovoviviparous. In his second paper (1959) he finds evidence from embryos " confirming that the insects are ovoviviparous ".

Hagan (1951) deals fully with the rather confused concepts of the terms " ovoviviparity " and " viviparity " in insects and brings forward a classification of the types of viviparity. He figures and describes in detail the embryonic development of *Arixenia jacobsoni*, which exhibits what he terms " pseudoplacental viviparity ". *Arixenia esau* resembles *A. jacobsoni* so closely that it seems unlikely that the two species would differ in this condition. Hagan will be followed here, for it seems there can be no doubt that the two species are viviparous. Johannsen and Butt (1941) do not deal with *Arixenia*.

Body Length

Although Cloudsley-Thompson (1957) said of his smallest nymphs of the two species of *Arixenia* that they " are so large and heavily chitinised that I feel convinced they represent the second instar ... ", he corrected this in his 1959 paper after dissecting material of *Arixenia esau*. However, the large size and heavy sclerotisation of the smallest specimens of these species would not, *ipso facto*, determine them as second instar, for *Arixenia* is one of the bulkiest of Dermaptera, and Hagan (1951), in fact, says of *A. jacobsoni* that the " parents give birth to relatively enormous offspring ... equipped with numerous setae ". Specimens which, for the reasons given below, the writer judges to be first instar nymphs among Harrison's Niah Caves material of *Arixenia esau* have an average total length of 1·3 cm., are heavily sclerotised and covered with bristles.

The abdomen of Dermaptera is telescopic and body length is therefore not a reliable measurement for growth studies, but it is useful as a guide to size (Giles, 1952). In this sense it is used in this paper. The ratios between the body lengths of first instar nymphs and adults of *Euborellia annulipes* (Lucas), 1847, *Marava arachidis* (Yersin), 1860 and *Forficula auricularia* L. are all approximately 1 : 3 (Hincks, 1948, Hincks, 1948 and Crumb *et al.*, 1941, respectively). Those of *Anisolabis littorea* and

Chelisoches morio (Fabricius), 1775 are about 1 : 4 (Giles, 1953 and Terry, 1905, respectively).

The ratio between the body lengths of the first instar specimens of *Arixenia esau* from Niah Caves, mentioned above, and of the adults is slightly under 1 : 3. The same ratio holds for similar material of *A. jacobsoni* among Hacker's specimens from Malay States, 1920. Although manifestly large, then, in absolute size, the first instar nymphs of *Arixenia* spp. bear a similar body length ratio to the adults as that of other species of Dermaptera. It would therefore be unwise to use size alone for assessing the smallest specimens as second instar.

The Antennae

The writer believes that the presence and the structure of the 8-annulate antennae are critical in the determination of the first instar of Dermaptera, but neither of these characters was considered by Cloudsley-Thompson (1957, 1959) in determining the instars of *Arixenia*. Table I lists the species of Forficulina, the condition of whose first instar antennae is known. It might be mentioned that all the families of the suborder are represented. The typical condition of the first instar antenna is thus undoubtedly 8-annulate.

TABLE I.—*Numbers of antennal annuli of the first and second instars of some Forficulina.*

Species	Numbers of antennal annuli		Authorities
	I Instar	II Instar	
Euborellia annulipes (Lucas) .	8 or 9[1]	11	Hincks (1948, 1956)
Euborellia ståli (Dohrn) . .	8	10	Cherian and Basheer (1940)
Anisolabis littorea (White) .	8	13 or 14	Giles (1952)
Labidura riparia truncata (Kirby) .	8[2]	15 or 16[2]	
Labia curvicauda (Motschulsky) .	8	9	Hincks (1956)
Marava arachidis (Yersin)	8[3]	10	Hincks (1948, 1956)
Sphingolabis hawaiiensis (de Bormans)	8	10	Marucci (1955)
Chelisoches morio (F.) .	8	12	Hincks (1948, 1956) Terry (1905, 1906)
Chelidurella acanthopygia (Gené) .	8	10	Lhoste (1942, 1957)
Forficula auricularia L. . .	8	10	Chapman (1917) Crumb *et al.* (1941) Henson (1947) Hincks (1956) Lhoste (1942, 1957)

[1] These figures are based on only 2 specimens (Hincks, 1948).
[2] Observations by writer during breeding experiments in connection with other work.
[3] Ramamurthi (1956) figures an embryo of this ovoviviparous species.

Further, according to the authorities given in Table I, in *Euborellia ståli* (Dohrn), 1864, *Anisolabis littorea*, *Labidura riparia truncata* (Kirby), 1903, *Marava arachidis*, *Chelisoches morio* and *Forficula auricularia* the first instar antenna consists of the scape and pedicel of the basal region, the meriston of the middle and the five long annuli of the apical region (Giles, 1952). There is every reason to believe that this is the typical condition of the first instar antenna of Forficulina.

The table also shows that moulting to second instar is accompanied by an increase in the number of annuli. This is known, from the workers cited there, to result from the division of the meriston in *Anisolabis littorea*, *Labidura riparia truncata*, *Chelisoches morio*, *Chelidurella acanthopygia* (Gené), 1832 and *Forficula auricularia*. It is undoubted that division of the meriston at moulting is also a general feature of the Forficulina.

Cloudsley-Thompson (1957, fig. 2) shows that the antennae of his smallest specimens of *Arixenia esau* and *A. jacobsoni* are 8-annulate and of typical form. It is also

readily apparent that moulting is accompanied by an increase in the number of annuli as a result of the division of the meriston.

It is obvious that the structure and method of growth of the antennae are identical in the Arixeniina and the Forficulina. Thus nymphs of *Arixenia* with 8-annulate antennae of the typical structure described above belong to the first instar, as was suggested by Cloudsley-Thompson (1959). Indeed, it seems to the writer that it would be an extraordinary circumstance, not to be lightly dismissed and requiring very close examination, if this were not so.

In addition, the writer has dissected the two females of *Arixenia esau* from the material examined by Cloudsley-Thompson. The internal preservation was good and
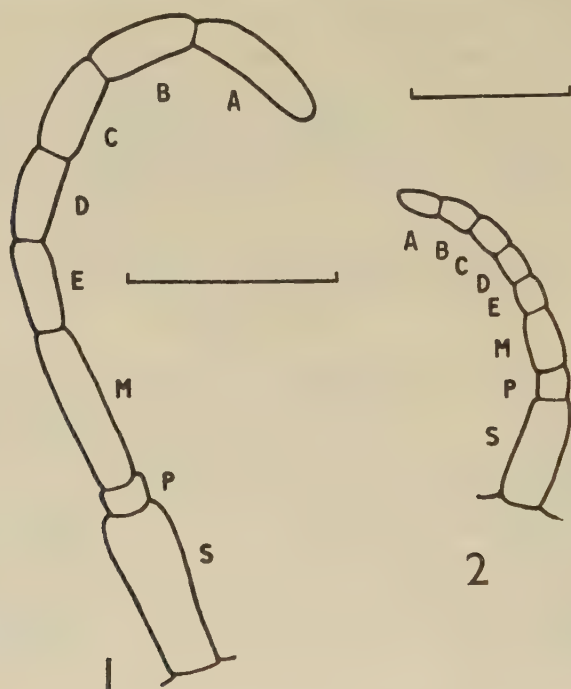
FIGS. 1–2.—Antenna of : (1) *Arixenia esau* embryo ; (2) *Hemimerus talpoides* embryo. *A–E*, annuli of apical region ; *M*, meriston ; *P*, pedicel ; *S*, scape. Scale lines represent 1 mm.

one proved to be gravid, four embryos being removed from follicular chambers of the ovarioles. There was no trace of chorion or other investment ; the embryonic cuticle was firm, the normal appendages were well-formed, but fairly large pregenital abdominal appendages were also present. All had antennae with eight annuli in the typical first instar condition (fig. 1). Dissection of three females of *A. esau* from the Niah Caves, Sarawak, provided larger, more advanced embryos ; their antennae had the same form.

It might be argued that the large size of the smallest nymphs of *Arixenia* spp. is due to prebirth moulting. The possibility of this is briefly discussed by Cloudsley-Thompson (1959) but he concludes, on the basis of head widths, that he " ... [does] not think this can be the case, although it is not impossible ". Perhaps prebirth moulting could take place but, in the absence of external stimuli, without division of the meriston. Under these circumstances an outburst of division by the meriston could be expected at the first moult after birth, but comparison of Tables I and II shows that this is not so. The absence of exuviae associated with the nymphs the

writer dissected from *A. esau* and the presence on them of the typical first instar 8-annulate antennae leads to the conclusion that prebirth moulting does not in fact take place.

THE LIFE CYCLE OF *Arixenia*

In *Arixenia esau*, then, there is no doubt that in reality the life cycle comprises four nymphal instars and the adult. This is in no way unusual and is the normal condition in many Dermaptera. The authorities cited in Table I have also worked out the life cycles of the listed species ; all have four nymphal instars except *Anisolabis littorea* and *Euborellia ståli* which have five, as does *Anisolabis maritima* (Gené), 1832 (Guppy, 1950), and data are not available for *Labidura riparia truncata*.

The 8-annulate antenna of *A. jacobsoni* would also belong to the first instar and this species' life-cycle would likewise consist of four nymphal instars and the adult.

Table II sets out the condition of the antennae and provides a means of determining the four nymphal instars and the adults of *Arixenia esau* and *A. jacobsoni*. Data on the antennal annuli are based on Cloudsley-Thompson (1957), except that his interpretation of the constitution of the middle region is not followed. (*See* p. 21). Middle region counts are given to enable determinations to be made on specimens with broken antennae.

TABLE II.—*Numbers of annuli in the antennae of nymphs and adults of both* Arixenia esau *and* A. jacobsoni.

Instar	Number of annuli	
	Middle region	Entire antenna
I	1	8
II	4	11
III	5	12
IV	6	13
♂	7	14
♀	7	14

THE FIRST INSTAR ANTENNAE OF *Hemimerus talpoides*

The writer has examined free-living specimens of *H. talpoides* having the typical 8-annulate antennae of the first instar of other Dermaptera. Three embryos were also dissected out of a female *H. talpoides* : they were well-developed, as evidenced by the absence of pregenital abdominal appendages and had antennae of the usual 8-annulate form (fig. 2). It is obvious that the first instar antenna of *H. talpoides* is of the typical 8-annulate form of other Dermaptera.

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THE SWAMP ENVIRONMENT AND THE BREEDING OF MOSQUITOES IN UGANDA

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Introduction

In Uganda, the number of mosquitoes which breed in swamps exclusively is very small (Goma, 1960). The vast majority of species only include swamps among their various breeding places. This observation seems to be general throughout the world, as can be concluded from the brief summaries of the literature on mosquito larval biology by Covell (1927), De Meillon (1947), Evans (1938), Hopkins (1952), Horsfall (1955) and Russell *et al.* (1943).

According to Beadle and Lind (1959), the various swamps of Uganda occupy some 5,000 square miles. These swamps constitute an environment which is extremely varied in regard to the ecology of mosquito larvae (Goma, *op. cit.*).

The object of the present paper is to describe the swamps of Uganda, in their natural, undisturbed state, as an environment for the breeding of mosquito larvae. Another paper dealing with the influence on mosquitoes of human activities which result in altering the swamp environment will appear elsewhere (Goma, 1961, *in press*).

Classification and General Description of Swamp Habitats

A number of authors (*e.g.* Eggeling, 1934, 1935 ; Bulman, 1952 ; Carter, 1955 ; Gibb *et al*, 1955 ; Goma, 1960) have suggested various classifications of the swamps of Uganda. However, with the exception of Goma, these authors were not concerned with classifying the swamps from the point of view of the ecology of mosquito larvae. According to Goma, the various swamps may be distinguished as permanent or seasonal ; or as composed principally of grass, papyrus, or sphagnum ; or as occurring at lake-edges, in rivers, or inland, or at high or low altitude. In the present paper an attempt is made to bring together the various suggestions into a single system.

Proposed classification

The major division in mosquito breeding places is perhaps between *permanent* and *transient* accumulations of water (Bates, 1949). On this basis, the various swamps of Uganda that provide breeding places for mosquito larvae may be divided broadly into two main groups, permanent swamps and seasonal swamps.

Three classes of permanent swamps may be distinguished :—(1) those occurring along the shores of lakes and large rivers, such as the Nile ; (2) those occurring in inland valleys, small rivers and streams, as well as those swamps which occupy certain old and extinct volcanic craters ; and (3) a group of swamps whose existence depends upon special chemical conditions : these are the acid, sphagnum swamps, which may occur along or near lakeshores, or in old and extinct volcanic craters.

Very little comprehensive work has been done on the larval ecology of swamp-breeding mosquitoes in Uganda and the actual factors which control the distribution of larvae in the various swamps are not fully understood. From the above considerations, however, it is proposed to classify the larval swamp habitats into two major groups, as follows :

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A. *Permanent swamps*
    (1) Littoral Swamps
    (2) Permanent Inland Swamps
    (3) Sphagnum Swamps

B. *Transient swamps*
    (4) Seasonal Inland Swamps.

(1) *Littoral swamps*

In this class are included the permanent swamps which occur along the shores of the various lakes, the Victoria Nile and the Albert Nile. Both Eggeling (1934, 1935) and Carter (1955) give detailed accounts of littoral swamps, particularly those fringing Lake Victoria. These swamps can be divided into a variable number of zones of characteristic vegetational communities, between the open lake water and the dry shore. The seven zones distinguished by Eggeling are : (*a*) nymphaea zone, (*b*) fringing papyrus, (*c*) fern and sedge, (*d*) *Limnophyton* swamp, (*e*) papyrus swamp, (*f*) *Miscanthidium* swamp and (*g*) *Phoenix* swamp. On the other hand, Carter recognises only four main zones : (*a*) the water-lily zone, (*b*) the fern and sedge zone, (*c*) the papyrus zone and (*d*) the grass swamp. The water-lily zone, or the fern and sedge zone, or both, may be absent ; and the papyrus, elephant grass, or *Miscanthidium* (as the case may be) may, therefore, abut directly on the open water. This has been observed in certain littoral swamps of Lakes Bunyonyi, Mutanda and Victoria, and of both the Victoria and Albert Niles. On the Nile, it is common to find *Pistia* and *Ceratophyllum* forming a zone which separates papyrus from the open water, sometimes only temporarily.

The various zones differ significantly in their biological conditions, which must affect the breeding of mosquito larvae in these habitats. For example, Carter (*op. cit.*) has shown that the water-lily zone is usually well oxygenated. On the other hand, the water in the papyrus zone is characterised by almost complete lack of oxygen (0 to 2 per cent. saturation), high CO_2 content (up to 57 p.p.m.) and higher organic matter content. The water of the grass swamp on the shore side of the papyrus is not noticeably different from that of the papyrus zone near the shore, but the grass swamp is generally dry except in rainy season. Littoral swamps, especially those fringing the lakes, are subject to considerable variation in their water level (Brooks, 1925). The constant swell on the lake and the more violent storms (Eggeling, 1935) must have a tremendous effect on the swamps and on the mosquito larvae inhabiting such swamps.

(2) *Permanent inland swamps*

This class includes the permanent swamps of the inland valleys and streams and those occurring in old extinct volcanic craters. The most extensive of these are papyrus swamps. The reed *Phragmites mauritianus* is one of the pioneer plants, especially in Western Uganda (Beadle and Lind, 1959), and some of the swamps in the Fort Portal area are dominated by this plant (Lind, 1956). Other swamps of the class are variously referred to as sedge swamps, *Miscanthidium* swamps, mixed swamps, etc., depending on the type of dominant vegetation present.

From the work of Carter (*op. cit.*), Beadle (1954, 1957, 1958*a*, 1958*b*) and Gibb *et al.* (1955), and from the author's own personal observations, the following would seem to be the salient features of permanent inland swamps that are of particular relevance to the breeding of mosquito larvae. The water in such swamps is, to a great extent, stagnant, but there is invariably a water current passing through the swamp down to its outlet. In the vast majority of swamps this is extremely slow but where there is a river, a stream or a definite channel through the central part of the swamp, or during floods, the current becomes fast. Between the clumps of papyrus and other

vegetation are pools of open water, above the floating mat, which are heavily shaded by the dense vegetation, and in which mosquitoes breed. There are, also, numerous breeding places which are choked with vegetation and, therefore, not quite " open ". Although the swamps are perennially waterlogged, some of these pools dry up completely during the dry weather. In the rainy season confluence of the pools may take place and, in exceptional floods, the whole swamp may be flushed through with a mass of water. Under such conditions, it is not unusual to notice mosquito larvae being carried downstream by the current.

The water in these permanent swamps, and particularly in papyrus swamps, is characterised by extreme lack of oxygen. Carter (*op. cit.*) found the oxygen content to be always low—not above 20 per cent. saturation and usually below 6 per cent. According to Beadle (1958*b*), the range 0–1 mg. oxygen/litre covers most of the values normally obtained in the field. This has been confirmed by the author, with respect to the actual breeding places of the larvae.

Another characteristic of these waters is the presence of heavy, brown (or reddish-brown, red, or darkish-brown) flocculent matter, with iridescent ferruginous surface scums. Other physico-chemical conditions, which may be supposed to affect mosquito breeding in these habitats, include high CO_2 contents, relatively high contents of nitrogenous compounds and organic matter, and high to very high contents of total iron (*see* Carter, *op. cit.*).

(3) *Sphagnum swamps*

In Uganda, *Sphagnum* swamps are not a common feature. They are found at Namanve and Luzira, both near Kampala (Eggeling, 1934, 1935) ; in Kashambya Valley, near Kabale (Gibb *et al.*, *op. cit.*; Lind, 1956) ; between Lake Nabugabo and Lake Victoria ; and in the crater of Mount Mgahinga (at 11,100 ft.) on the Uganda-Congo border. The dominant plant in these swamps is the bog-moss, *Sphagnum*, and they appear to be associated with *Miscanthidium* (grass) swamps (Eggeling, 1934, 1935 ; Lind, 1956 ; Beadle and Lind, 1959) especially in the lowland valleys.

Sphagnum swamps occur in contact with ground water of low salinity (Beadle and Lind, 1959). Like the peat bogs in the Northern Hemisphere, their chief chemical characteristic is the high acidity of the water. In the swamp separating Lake Nabugabo from Lake Victoria, the *pH* varies from 3·5 to 4·5 (Beadle and Lind, *op. cit.*) ; although higher values (6·1) have been obtained, especially on the lake-fringe (Hopkins, 1952).

(4) *Seasonal inland swamps*

These swamps occur extensively in, and are very characteristic of, the northern parts of Uganda, *e.g.* Teso District. They are grass swamps and occur in floodplains and are only seasonally flooded. As stated by Gibb *et al.* (*op. cit.*), in general, it may be said that seasonal swamps are wet during the period April to October inclusive. For the other five months they are generally dry to very dry, according to the amount of rainfall in the dry season. Some exceptions to this generalization occur.

In the seasonal swamps, the micro-relief is often very broken by the occurrence of " tussock mounds " (Gibb *et al.*, *op. cit.*). These mounds are produced by the casting of swampworms, of which three species have been recognised—*Glyphodrilus* sp., *Alma stuhlmanni* and *Alma emini* (Wasawo and Visser, 1959). Fresh wormcasts show higher values than the parent soil with respect to all exchangeable ions (except that of aluminium), carbon, nitrogen and the C/N ratio. Only the ash content is lower, which indicates a greater percentage of organic material in the casts. Ideal breeding places are found between the mounds during the wet season and considerable quantities of fresh wormcasts occur in many of them.

The Breeding of Mosquito Larvae in the Various Swamp Habitats

In a recent paper, Goma (1960) has summarised the recorded swamp habitats of individual mosquito species known to breed in the swamps of Uganda. The reader is referred to this paper for such information. The present section is concerned mainly with the general nature of the mosquito fauna of each of the four classes of swamp described.

Table I shows the distribution of larval occurrence in the four major classes of swamp habitats ; and Table II shows the resemblances between these classes. These tables are based largely on data in Goma's (1960) paper ; they do not take into account those species on which there is too little information for the classification of their habitats, nor do they include the 14 unrecognised species of Goma's paper.

Table I.—*Occurrence of larvae in the four classes of swamp habitats*

	Class of swamp habitats			
	Littoral swamps	Permanent inland swamps	Seasonal inland swamps	*Sphagnum* swamps
Anopheles (*Anopheles*) *coustani* Lav.	+	+	+	+
A. (*A.*) *symesi* Edw.	+	.	.	.
A. (*A.*) *implexus* (Theo.)	.	+	+	.
A. (*Myzomyia*) *kingi* Christ.	.	+	.	.
A. (*M.*) *funestus* Giles	+	+	+	.
A. (*M.*) *rivulorum* Leeson	+	.	.	.
A. (*M.*) *rivulorum* var. *garnhamellus* Evans & Leeson	+	.	.	.
A. (*M.*) *marshalli* (Theo.)	.	+	.	.
A. (*M.*) *marshalli* var. *gibbinsi* Evans	.	+	.	.
A. (*M.*) *moucheti* Evans	+	.	.	.
A. (*M.*) *wellcomei wellcomei* Theo. (= *distinctus* var. *ugandae* Evans)	+	.	.	.
A. (*M.*) *christyi* (Newst. & Cart.)	.	+	.	.
A. (*M.*) *gambiae* Giles	.	+	+	.
A. (*M.*) *pharoensis* Theo.	+	+	+	.
A. (*M.*) *squamosus* Theo.	+	.	.	.
Hodgesia sanguinea Theo.	+	.	.	.
H. cyptopus Theo.	+	+	+	.
Uranotaenia pallidocephala Theo.	+	+	+	.
U. ? alboabdominalis Theo.	+	.	.	.
U. balfouri Theo.	+	+	+	.
U. chorleyi Edw.	+	+	.	.
U. hopkinsi Edw.	.	+	+	.
U. mashonaensis Theo.	+	+	.	.
Aëdomyia africana Nev.-Lem.	+	.	.	.
Aë. furfurea End.	+	+	.	.
Ficalbia (*Mimomyia*) *splendens* (Theo.)	+	.	.	.
F. (*M.*) *hispida* (Theo.)	+	+	.	.
F. (*M.*) *hispida* var. *sunyaniensis* Edw.	+	.	.	.
F. (*M.*) *lacustris* Edw.	+	+	+	.
F. (*M.*) *perplexens* Edw.	+	.	.	.
F. (*M.*) *pallida* Edw.	+	.	.	.
F. (*M.*) *mimomyiaformis* (Newst.)	+	.	.	.
F. (*M.*) *plumosa* (Theo.)	+	+	.	.
F. (*Etorleptiomyia*) *mediolineata* (Theo.)	+	+	.	.
F. (*Ficalbia*) *uniformis* (Theo.)	+	.	.	.
F. (*F.*) *malfeyti* Newst.	+	.	.	.
Mansonia (*Coquillettidia*) *metallica* (Theo.)	+	+	.	.
M. (*C.*) *versicolor* (Edw.)	.	+	+	.
M. (*C.*) *fuscopennata* (Theo.)	+	+	.	.
M. (*C.*) *aurites* (Theo.)	+	.	.	.
M. (*C.*) *microannulata* (Theo.)	+	+	.	.

	Class of swamp habitats			
	Littoral swamps	Permanent inland swamps	Seasonal inland swamps	*Sphagnum* swamps
M. (C.) *fraseri* (Theo.)	+	.	.	.
M. (*Mansonioides*) *africana* (Theo.)	+	+	.	.
M. (M.) *uniformis* (Theo.)	+	+	.	.
Aëdes (*Mucidus*) *mucidus* (Karsch.)	+	.	.	.
Aë. (*Aëdimorphus*) *punctothoracis* (Theo.)	+	.	.	.
Aë. (A.) *domesticus* (Theo.)	+	.	+	.
Aë. (A.) *tarsalis* (Newst.)	+	.	.	.
Aë. (A.) *albocephalus* (Theo.)	+	.	+	.
Aë. (A.) *gibbinsi* Edw.	+	.	.	.
Aë. (A.) *quasiunivittatus* (Theo.)	+	+	.	.
Aë. (A.) *dentatus* (Theo.)	+	.	.	.
Aë. (*Neomelaniconion*) *lineatopennis* (Ludl.)	+	+	+	.
Aë. (N.) *circumluteolus* Theo.	+	+	+	.
Culex (*Lutzia*) *tigripes* Grp.	+	+	+	.
C. (*Neoculex*) *andreanus* Edw.	+	.	+	.
C. (N.) *kingianus* Edw.	+	.	.	.
C. (N.) *rubinotus* Theo.	+	+	+	.
C. (N.) *insignis* (Cart.)	+	.	.	.
C. (*Culiciomyia*) *semibrunneus* Edw.	+	.	+	.
C. (*Culex*) *poicilipes* Theo.	+	+	+	.
C. (C.) *bitaeniorhynchus* Giles	+	+	+	.
C. (C.) *ethiopicus* Edw.	+	+	+	.
C. (C.) *aurantapex* Edw.	+	.	.	.
C. (C.) *annulioris* Theo.	+	+	+	.
C. (C.) *duttoni* Theo.	+	+	.	.
C. (C.) *theileri* Theo.	+	.	.	.
C. (C.) *univittatus* Theo.	+	+	+	.
C. (C.) *pipiens* L.	+	+	.	.
C. (C.) *zombaensis* Theo.	+	.	.	.
C. (C.) *ninagongoensis* Edw.	.	+	.	+
C. (C.) *chorleyi* Edw.	+	+	.	.
C. (C.) *quasiguiarti* Theo.	+	.	.	.
C. (C.) *decens* Theo.	+	+	+	.
C. (C.) *perfuscus* Edw.	+	.	+	.
C. (C.) *guiarti* Blanch.	+	+	+	.
C. (C.) *ingrami* Edw.	+	.	.	.
C. (C.) *grahami* Theo.	+	.	+	.
Total 78	69	42	27	2

TABLE II.—*Species composition of the four classes of swamp habitats*

Class of swamp habitats	Total no. of spp. recorded in class	No. of spp. "endemic" to class	No. of same spp. also recorded in class			
			Littoral swamps	Permanent inland swamps	*Sphagnum* swamps	Seasonal inland swamps
Littoral swamps	69	31	.	33	1	23
Permanent inland swamps	42	4	33	.	2	22
Sphagnum swamps	2	0	1	2	.	1
Seasonal inland swamps	27	0	23	22	1	.

From Table I it will be observed that only one species, *Anopheles coustani*, occurs in all the four classes. Some of the species are widely distributed, but others are "endemic" to particular classes of swamp.

Littoral swamps

Of the 78 species listed in Table I, 69 have been recorded breeding in littoral swamps and of these, 31 are " endemic " to the class ; 33, 23, and 1, of the other species, also occur in permanent inland, seasonal inland, and *Sphagnum* swamps, respectively.

Observations have been made on representative littoral swamps on the shores of Lakes Bunyonyi, Kioga, Mutanda, Nabugabo and Victoria, of the Kazinga Channel (joining Lakes Edward and George), the Albert Nile and the Victoria Nile.

In littoral swamps, certain mosquitoes occur most frequently only in certain types of breeding place. For example, situations where papyrus, reeds, short grass, or other vegetation are growing in quite clear, shallow water are preferred by *Anopheles funestus* (Leeson, 1937 ; Garnham *et al.*, 1948), *A. distinctus* var. *ugandae* (Gillett 1955), *Ficalbia lacustris* and *Culex aurantapex* (Hopkins, 1952), *Aëdes albocephalus* and *Aë. dentatus*. On the other hand, larvae of *A. coustani*, *C.* ? *invidiosus* Theo., *C. poicilipes*, *C. univittatus* group, *F. mediolineata* and *F. uniformis* have been found breeding in very turbid, shallow water, among elephant grass (*Pennisetum*).

The most productive habitats at the inner or lakeward side of littoral swamps are those containing *Pistia* and/or *Ceratophyllum*. Species which are most prevalent in such places are *Anopheles coustani*, *A. pharoensis*, *A. rivulorum*, *A. rivulorum* var. *garnhamellus*, *A. squamosus*, *Aëdomyia africana*, *Culex poicilipes*, *Ficalbia malfeyti*, *F. uniformis*, *F. splendens*, *Mansonia africanus* and *M. uniformis*. Hancock (1934) records the breeding of *A. coustani*, *C. univittatus*, *F. uniformis*, *Hodgesia cyptopus*, *Uranotaenia balfouri* and *U.* ? *pallidocephala* in a fern zone, at Namanve Swamp. In this type of habitat, larvae occur chiefly among the fern and not in the more open pools. However, observations made on Lakes Bunyonyi, Mutanda and Victoria indicate that vast stretches of the vegetational zones bordering on the open lake are extremely unproductive. Prodigious numbers of shrimps occur in such habitats ; but there is no direct evidence that these are responsible for the absence of mosquito larvae.

The mosquito fauna nearer the dry land is generally quite different from that at the lakeward side. For example, *Culex rubinotus*, *C. guiarti*, *C. chorleyi*, *C. tigripes*, *Aëdes gibbinsi*, *Aë. lineatopennis*, *Aë. circumluteolus*, *F. hispida*, *H. cyptopus*, *U. mashonaensis*, and certain *Mansonia* (*Coquillettidia*) spp. occur only nearer the dry land, but Anophelines are very rare in, and often absent from, such habitats.

Permanent inland swamps

Table I shows that, of the 78 species listed, 42 have been found breeding in permanent inland swamps. From Table II, it will be seen that only 4 are " endemic " to the class, and that, of the rest, 33, 22, and 2 species also occur in littoral, seasonal inland, and *Sphagnum* swamps, respectively.

Observations have been made on representative swamps of the class, in Ankole, Busoga, Kigezi, Mengo, Teso and Toro Districts, but only the papyrus swamps in the neighbourhood of Kampala, Mengo District, have been intensively investigated.

In the neighbourhood of Kampala, intensive studies have been made on Kaazi-Road, Kamilangoma, Lubigi, Mayanja, and Namulonge Swamps. The most prevalent species breeding inside the swamps are *Culex decens*, *C. univittatus* group, *C. tigripes*, *C. rubinotus*, *Ficalbia hispida*, *F. lacustris*, *F. plumosa*, *F. mediolineata*, *Hodgesia cyptopus*, *Uranotaenia balfouri*, *U. mashonaensis*, *U. pallidocephala*, *Mansonia africanus*, *M. uniformis* and *M. fuscopennatus*. They breed in water with extremely little oxygen (values of 0 to 0·88 mg. oxygen/litre are most common), containing light to heavy flocculence (brown, reddish-brown or red, to darkish-brown in colour), with very thin to thick ferruginous surface scums. Occasional and rather sparse breeders in such habitats include *C. duttoni*, *C. pipiens*, and *F. hispida* var. *sunyaniensis* : the first in shallow, turbid, foul-smelling water, and the second in pools choked with

vegetation. At the periphery, larvae of *Aëdomyia furfurea*, *Anopheles coustani*, *A. gambiae*, *A. funestus*, *C. guiarti* and *C. poicilipes* occur where the water is clear, shallow, and exposed to full sunlight; while those of *C. annulioris* are found only in the presence of green filamentous algae. Records and observations elsewhere in Uganda show this to be the general pattern of larval occurrence.

A few species have been found breeding only in swamps at high altitudes, e.g. *Anopheles marshalli*, *A. marshalli* var. *gibbinsi* (both at 5,500 ft.) and *A. ardensis* (Theo.) (6,000–7,000 ft.), in Ankole District; *A. kingi*, *C. chorleyi* and *Aëdes quasi-univittatus* (all above 6,000 ft.), in Kigezi District. However, there are a number of other species which occur at both high and low altitudes, e.g. *A. coustani*, *C. annulioris*, *C. rubinotus*, *C. tigripes*, *Uranotaenia balfouri* and *U. ? alboabdominalis*.

Not much work has been done on the crater swamps, within this class, but according to Hopkins (1952), *U. balfouri* occurs not uncommonly in Toro District in old craters filled with papyrus swamp, in open patches among the floating liverwort, *Riccia*. *U. mashonaensis* is found in similar habitats, but particularly among *Lemna*.

Sphagnum swamps

These produce less mosquito larvae than any other Uganda swamps. Tables I and II show that only two species have been recorded breeding in them and there are no " endemic " species. Four other unrecognised species, however, have been recorded by the author from these swamps.

Only two *Sphagnum* swamps have been investigated. These are (*a*) the swamp between Lakes Nabugabo and Victoria, and (*b*) the swamp filling the old volcanic crater on Mt. Mgahinga, at 11,100 ft., on the Uganda-Congo border. *Anopheles coustani* (Hopkins, 1952; Goma, 1960), *Culex* sp., *Ficalbia* sp. and *Mansonia* sp. have been recorded in (*a*); and *C. ninagongoensis* and *Culex* sp. (Goma, *op. cit.*) in (*b*). There is very little other animal life in these waters. Some *Spirostomum* (Protozoa), Notonectid and Belostomatid bugs, beetles and tadpoles occur rather sparsely here and there.

Seasonal inland swamps

Of the 78 species listed in Table I, 27 have been found breeding in seasonal inland swamps. From Table II, it will be seen that there are no species which are "endemic " to the class but 23, 22, and 1 occur in littoral, permanent inland and *Sphagnum* swamps, respectively.

Observations have been made on representative swamps of the class in Masaka, Mengo and Teso Districts. On the whole, these swamps have been far less studied than the permanent inland swamps and the littoral swamps.

The most intensively studied swamp in this class is Nakazi Swamp, just beyond 12 miles from Kampala on the road to Bombo. It is a grass-dominated swamp. Where papyrus occurs it is largely semi-permanent. Larvae of *Aëdes lineatopennis*, *Culex rubinotus* and *Uranotaenia balfouri* breed in pools between mounds growing *Miscanthidium violaceum*. Under the heavy shade provided by palm-trees reinforced by tall grass, occur larvae of *Anopheles implexus*. Other species breeding in the various swamp pools include *A. coustani*, *C. tigripes* and *U. pallidocephala*. *Ficalbia hispida*, *F. mediolineata*, *F. plumosa* and *U. mashonaensis* appear to occur most prevalently where the breeding pools are choked with grass and sedge (*Cyperus latifolius*). In the more exposed parts of the swamp, among short grass, profuse breeding of *A. gambiae*, *C. decens* and *C. univittatus* occurs in shallow pools. *C. annulioris* breeds only in the presence of *Spirogyra*.

Elsewhere, very sparse breeding of mosquito larvae has been observed, but breeding occurs invariably in shallow water that is clear to slightly flocculent, between natural mounds.

The main grass swamps between Masaka and Bukakata appear to be burnt seasonally, and in some of them *Sphagnum* is developing in patches. In such places, very sparse breeding of *Aëdes domesticus, Anopheles coustani* and *Culex* sp. has been recorded. These mosquitoes have also been found breeding where the arrowhead, *Sagitaria* grows in the pools, and among the grass *Loudetia fragmitoides*.

In the seasonal grass swamps of Teso District, the present author has recorded the breeding of only two species, *A. gambiae* and *U. mashonaensis* : the first, in a " clayey " pond, containing very turbid and foul water, inside Kajonyi Swamp ; and the second, in water containing heavy brown flocculence, between tussock mounds, in Ochuloi (Omusogo) Swamp. Both swamps are near Soroti. In many of the potential breeding places, there are considerable amounts of fresh wormcasts, but whether these affect the breeding conditions is not known.

DISCUSSION

The swamps of Uganda, as an environment for the breeding of mosquito larvae, may be grouped into four major classes : (1) littoral swamps, (2) permanent inland swamps, (3) *Sphagnum* swamps and (4) seasonal inland swamps. This classification, although it may appear to be somewhat arbitrary, is quite satisfactory when considering the general biology and distribution of swamp-breeding mosquitoes in this country. Its chief disadvantage, however, seems to be the overlapping of the various types of habitat. For example, it is difficult to decide whether inland swamps that are only dry for a very short period of the year should be regarded as belonging to (2) or to (4) above. The *Sphagnum* swamp between Lakes Nabugabo and Victoria fringes on the former lake very extensively and so may be regarded as partly littoral. On the other hand, the *Sphagnum* swamps occurring at high altitudes in small extinct volcanic craters are closely related to the crater swamps which have been included in the class of permanent inland swamps, but because of their very specialised chemical (acid) conditions and the nature of their mosquito fauna (*see below*) it has seemed reasonable to consider all *Sphagnum* swamps as forming a distinct class of their own.

A study of Tables I and II shows the faunal distinctiveness of the four major classes of the swamp environment described. Of the 78 species listed, 69 occur in littoral swamps, 42 in permanent inland swamps, 2 in *Sphagnum* swamps and 27 in seasonal inland swamps ; 31 species are "endemic " to littoral swamps and 4 to permanent inland swamps. The other two classes have no " endemic " species. Only one species, *Anopheles coustani*, occurs in all the four classes. Littoral swamps and permanent inland swamps have more species in common than either class has with seasonal inland swamps, but the seasonal inland swamps have about the same *number* of species in common both with littoral swamps and with permanent inland swamps. Although littoral swamps have the greatest number of mosquito species, in our experi ence, permanent inland swamps seem to produce more individuals per species than do littoral or seasonal inland swamps. The *Sphagnum* swamp class has the lowest numbers both of species and of individuals.

The expectation that the hydrogen ion concentration of the environment might prove to be of outstanding importance to animal life has not been realised (Allee *et al.*, 1950). The hypothesis of a major division of mosquito larvae into acidophile and alkalinophile species is generally untenable, but in Uganda the low productivity of the *Sphagnum* swamps, which are acid, is in agreement with observations in other parts of the world (in the Soviet Union : Adowa, Nikitinsky and Sebenzow, 1927 ; Adowa and Ravitsch-Tscherbo, 1927 ; Smorodinzew and Adowa, 1927 ; Smorodinzew, Sebenzow and Adowa, 1928 ; in the United States of America : Frohne, 1942 ; Knutson, 1943). On the other hand, Metz (1918) reports the profuse breeding of *A. crucians* in an extensive, shallow swamp, containing water so far polluted with the chemical waste of a sulphuric acid factory as to be inimical to fish and to aquatic vegetation other than algae.

The actual factors controlling the distribution of mosquitoes in the various swamps of Uganda are not fully understood. In the littoral, permanent inland and sphagnum swamps, breeding places are available throughout the year, but not in the seasonal inland swamps. It is not known whether any species prevalent in the latter swamps undergo diapause during the dry (or " non-breeding ") season, but homodynamy seems to occur in the vast majority of species if not in all, and it is, perhaps, significant that none of the species is " endemic " to seasonal inland swamps.

It has been suggested that those species which have a marked preference for moderately clean water occur more frequently in littoral swamps (Goma, 1960). However, it is not unusual to find even those species that are " endemic " to the class breeding in very foul and obviously extremely deoxygenated water, e.g. *Aëdomyia africana*, *Ficalbia splendens*, *F. malfeyti* and *F. uniformis*.

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One asterisk (*) at the end of a reference citation means that an abstract only was consulted, in the *Review of Applied Entomology* (B). Two asterisks (**) mean that an abstract only was consulted, in the *Tropical Diseases Bulletin*.

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SELECTION OF MATERIALS FOR CASE-BUILDING BY LARVAE OF CADDIS FLIES (TRICHOPTERA)

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INTRODUCTION

LITTLE work has been done on the selection of materials for case-building by caddis larvae. The majority of published observations are brief and unsupported by detailed experimental work.

Buchner (1905) considered that *Drusus* selected pine needles and *Limnephilus stigma* Curtis seeds of water plants because these materials were distasteful to predators, but he gave no evidence to support this. Bierens de Haan (1922) showed that the larvae of *L. marmoratus* Curtis preferred spruce needles to other material. Uhlmann (1924) found that young larvae of *Phryganea grandis* L. preferred stems to other material, although they were able to use leaves or sand in the absence of stems, and he suggested that this preference might change as the larvae grew older. Dodds and Hisaw (1925) thought that the selection of materials might be based on the form and size of the pieces. Gorter (1929) showed that the larvae of *Limnephilus flavicornis* (Fab.) preferred pine needles to other materials. Brues (1930) thought that vision might play an important role in the selection of the shining opal flecks which he found in the cases of *Hesperophylax magnus* Banks. Gorter (1931) studied the selection of materials by 11 species of caddis larvae and found that older larvae showed a narrower range of choice than younger ones. Scheffler (1932) suggested that the choice of materials might be determined by the nature of the water in which the larvae lived. Uhlmann (1932) suggested that whether a larva selected sand or plant material was determined genetically. Dembowski (1933) measured a few sand grains at the anterior and posterior ends of the case of *Molanna angustata* Curtis and concluded that the larva selected larger sand grains as they grew older. Moretti (1934) showed that colour did not play an important role in the selection of materials by *L. rhombicus* (L.), *Glyphotaelius pellucidus* (Retzius) and *Sericostoma personatum* (Spence) and he thought that shape and dimension were more significant. Fankhauser and Reik (1935) suggested that larvae of *Neuronia postica* Walker preferred material that could be used without cutting, and they observed that the larvae preferred dead leaves to all other materials. Copeland and Crowell (1937) noted that a species of *Limnephilus* selected material of suitable length. Fritsch (1941) gave *L. flavicornis* and *L. bipunctatus* Curtis sand grains of four graded sizes and found that certain sizes were preferred. Dudziak (1950) suggested that the thickness of the material was of significance in selection by larvae of *Phryganea obsoleta* Hagen. Staropolska and Dembowski (1950) observed that *M. angustata* selected larger pieces of chicken egg shells for building the hood than for the rest of the case. Maillet and Carasso (1952) found that the larvae of *Triaenodes conspersa* (Rambur) preferred rigid twigs of small diameter for building the normal case.

It will be seen, therefore, that observations on the selection of material are scattered and inadequate and no general survey has been made. Apart from the work of Dembowski (1933) and of Fritsch (1941), there has been no quantitative study of the problem.

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This work was based on 38 species representative of all British families the larvae of which build portable cases (*see* Table I). The localities where the larvae were collected are listed in an unpublished thesis (Hanna, 1956). The classification adopted is that of Mosely (1939), with the alterations in generic names suggested by Kimmins (1949, 1952, 1956).

The larvae were pushed out of their cases and provided with a variety of materials, which included : *Ceratophyllum*, grass, dead leaves, bark, sand grains of different sizes and small stones. The larvae were watched as they built new cases and for each species a record was made of the material chosen in preference to all others. This preferred material was then eliminated and the larva watched to see which of the remaining materials was chosen. This process was repeated with all the possible materials and an order of preference of materials for building the normal case was thus recorded.

In another group of experiments the larva was provided with material which was not the one naturally favoured and was allowed to use this in one of the following two ways : (1) When the larva had constructed a new case, it was pushed out and the case removed and this process was repeated several times ; (2) the young larva in its case was provided with this material until it became fully grown.

The naturally preferred material was then added, and the behaviour of the larva watched. In each of these experiments about fifty larvae were examined.

A quantitative study has also been carried out on the following 14 species : *Trichostegia minor* (Curt.), *Agrypnia pagetana* Curt., *P. varia* Fab., *Oligotricha ruficrus* (Scop.) and *P. grandis* L. (Phryganeidae) ; *Limnephilus centralis* Curt., *L. vittatus* (Fab.), *L. fuscicornis* (Rambur), *Potamophylax stellatus* (Curt.) and *Chaetopteryx villosa* (Fab.) (Limnephilidae) ; *Notidobia ciliaris* (L.) and *Silo nigricornis* (Pictet) (Sericosto-matidae) ; *Beraea maurus* (Curt.) (Beraeidae) ; *Athripsodes cinerea* (Curt.) (Lepto-ceridae).

The young phryganeid larvae were pushed out of their cases and supplied with *Ceratophyllum*. Cases of different sizes were then broken up and the pieces of *Cerato-phyllum* counted and measured for length. For *T. minor* and *P. varia* four or five cases were examined for each millimetre length class and the pieces of *Ceratophyllum* measured to the nearest 0·5 mm. As there was little variation between cases of the same length class, it was considered sufficient to measure one case only in each. This procedure was therefore followed for the remaining three species of Phryganeidae. The tables and histograms containing these results are included in an unpublished thesis (Hanna, 1956).

The other species studied built their cases of sand grains and, as they can use grains of any size in the absence of that most favoured, it was decided to examine cases collected in the field. The larvae were pushed out of their cases, which were then washed, dried and weighed. The cases were then broken into pieces and the number of sand grains recorded. Five cases were examined in each length class and the mean weight of the sand grains then calculated.

RESULTS

Qualitative studies

The order of preference observed in the selection of material for case-building is shown in Table I.

Larvae of all species studied, when deprived of the material which they prefer and compelled to use alternatives for their cases, always chose their favourite material when it was again available.

Quantitative studies

According to the type of material used the larvae I have examined fall into two main groups :

(1) *Larvae that build cases of plant materials.*—This group includes all the species examined in the Phryganeidae. They can be subdivided into :
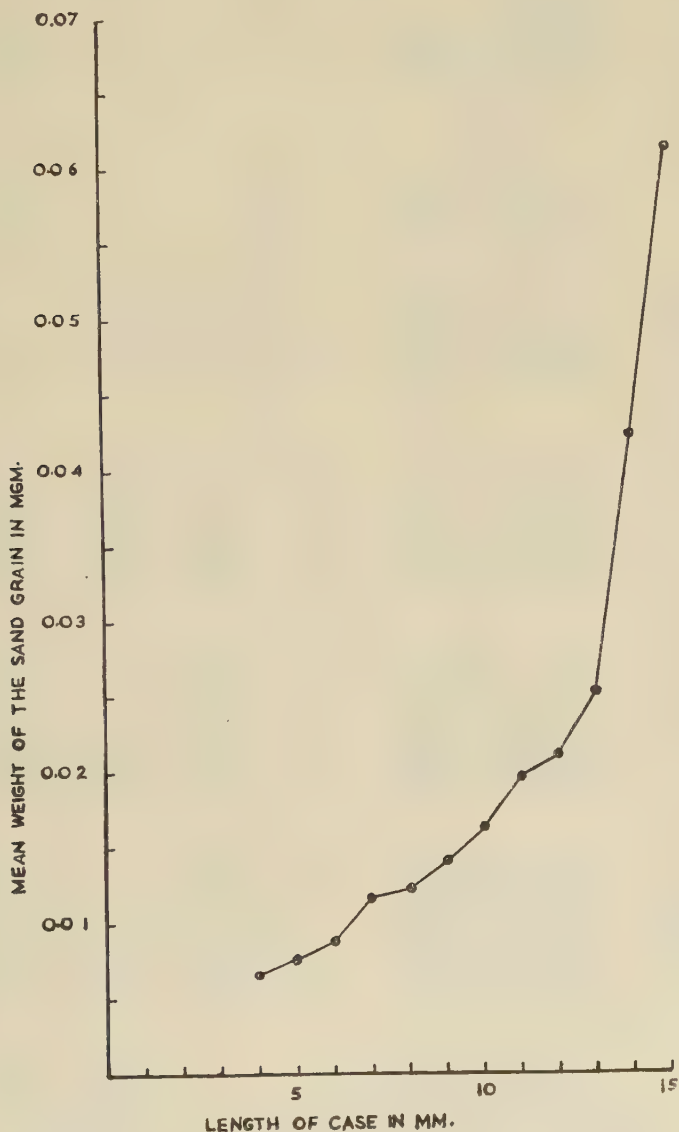

Fig. 1.—The relation between weight of sand grain and length of larval case of *Notidobia ciliaris* L.

(a) *Trichostegia minor*, *Agrypnia pagetana*, and *Oligotricha ruficrus.*—The larvae tended to select longer pieces of *Ceratophyllum* as they grew older.

(b) *Phryganea varia* and *P. grandis.*—The larvae selected progressively longer pieces of *Ceratophyllum* until they were nearly half grown, when there was a tendency to select pieces approximately equal in length.

TABLE I.—*The order of preference observed in selecting material for case-building*

Species	Order of preferences						
	1	2	3	4	5	6	7
PHRYGANEIDAE							
Trichostegia minor	Dead leaves	Bark	Ceratophyllum	Elodea leaves	Grass	Sand grains	.
Agrypnia pagetana	Elodea leaves	Ceratophyllum	Elodea stems	Bark	Grass	Sand grains	.
Phryganea varia (up to 9 mm. long)	Ceratophyllum	Elodea leaves	Dead leaves	Elodea stems	Sand grains	.	.
(older larvae)	Dead leaves	Elodea leaves	Elodea stems	Ceratophyllum	Grass	Dead leaves	Sand grains
Oligotricha ruficrus (up to 7 mm.)	Ceratophyllum	Elodea leaves	Elodea stems	Bark	Grass	Sand grains	Sand grains
(older larvae)	Dead leaves	Elodea leaves	Bark	Elodea stems	Ceratophyllum	Dead leaves	Sand grains
Phryganea grandis (up 6 mm.) and P. striata (up to 9 mm.)	Ceratophyllum	Elodea stems	Elodea leaves	Dead leaves	Bark	Grass	Sand grains
P. grandis and P. striata (older larvae)	Dead leaves	Elodea stems	Elodea leaves	Bark	Grass	Ceratophyllum	Sand grains
LIMNEPHILIDAE							
Glyphotaelius pellucidus	Dead leaves	Reed	Elodea leaves	Elodea stems	Grass	Ceratophyllum	Sand grains
Limnephilus flavicornis	Elodea stems		Elodea leaves	Elodea stems	Grass	Then no selection was observed	
L. lunatus	No selection was observed						
L. centralis	Large sand grains	Small stones	Fine sand grains	Dead leaves			
L. vittatus	Fine sand grains	Large sand grains	Small stones	Elodea leaves			
L. fuscicornis	Large sand grains	Small stones	Fine sand grains	Dead leaves			
Anabolia nervosa (up to 7 mm.)	No selection was observed						
(older larvae)	Dead leaves	Bark	Elodea stems	Elodea leaves			
Halesus radiatus	Bark	Dead leaves	Elodea stems	Elodea leaves	Sand grains		
Potamophylax stellatus (up to 7 mm.) / P. latipennis (up to 9 mm.) / Chaetopteryx villosa	No selection was observed						
Older larvae of three preceding species	Small flattened stones	Small irregular stones	Large sand grains	Broken shells	Bark	Fine sand grains	
Drusus annulatus	Large sand grains	Small stones	Fine sand grains	Dead leaves			
Apatania muliebris	Large sand grains	Small stones	Fine sand grains				
SERICOSTOMATIDAE							
Sericostoma personatum and Notidobia ciliaris	Large flattened sand grains	Large rough sand grains	Small stones	Fine sand grains			

SERICOSTOMATIDAE (continued)

Species						
Goëra pilosa and *Silo nigricornis*						
a—(tubular part of case)	Large sand grains	Fine sand grains	Small stones / Large sand grains			Sand grains
b—(side stones of case)	Flat stones on their inner surface and arched at outer margin	Small irregular stones	Large sand grains			
Brachycentrus submubilus	*Ceratophyllum*	Dead leaves	*Elodea* stems / Small stones / Sand grains	Grass / Bark	*Elodea* leaves / Dead leaves	Bark
Crunoecia irrorata (young larvae)	Fine sand grains	Large sand grains	Small stones / Sand grains	Dead leaves		
(older larvae)	Rectangular pieces of bark	Rectangular pieces of dead leaves	Bark			
Lepidostoma hirtum (young larvae)	Fine sand grains	Large sand grains	Small stones / Sand grains	Dead leaves	Dead leaves	
(older larvae)	Dead leaves	Bark	Bark			
Beraea maurus	Fine sand grains	Large sand grains	Small stones			
Beraeodes minuta	Fine sand grains	Large sand grains	Small stones			
Molanna angustata	Large sand grains	Small stones	Fine sand grains			
Odontocerum albicorne	Large flattened sand grains	Large rough sand grains	Small stones	Fine sand grains		
Athripsodes aterrima, *A. cinerea* and *Oecetis lacustris*	Fine sand grains	Large sand grains	Small stones			
Triaenodes bicolor	*Ceratophyllum*	*Elodea* leaves	*Elodea* stems / Small stones	Grass / *Elodea* leaves	Dead leaves	Sand grains
Mystacides nigra and *M. longicornis*	Fine sand grains	Large sand grains	Small stones / Sand grains			
Agapetus fuscipes	Sharp edged sand grains and stones					
Glossosoma boltoni (sides of case)	Small flattened stones	Small irregular stones	Large sand grains	Fine sand grains		
(floor of case)	Large sand grains	Small stones	Fine sand grains			

BERAEIDAE

MOLANNIDAE

ODONTOCERIDAE

LEPTOCERIDAE

RHYACOPHILIDAE

The young larvae of Phryganeidae, except *T. minor*, used occasional longer pieces so that their cases tended to be ragged in appearance. These longer pieces were not found in cases of older larvae which therefore appeared much neater.

(2) *Larvae that build their cases of sand grains.*—This group can be subdivided into :

(a) *Notidobia ciliaris, Silo nigricornis, Beraea maurus* and *Athripsodes cinerea.*—The larvae used progressively larger sand grains as they grew (fig. 1).
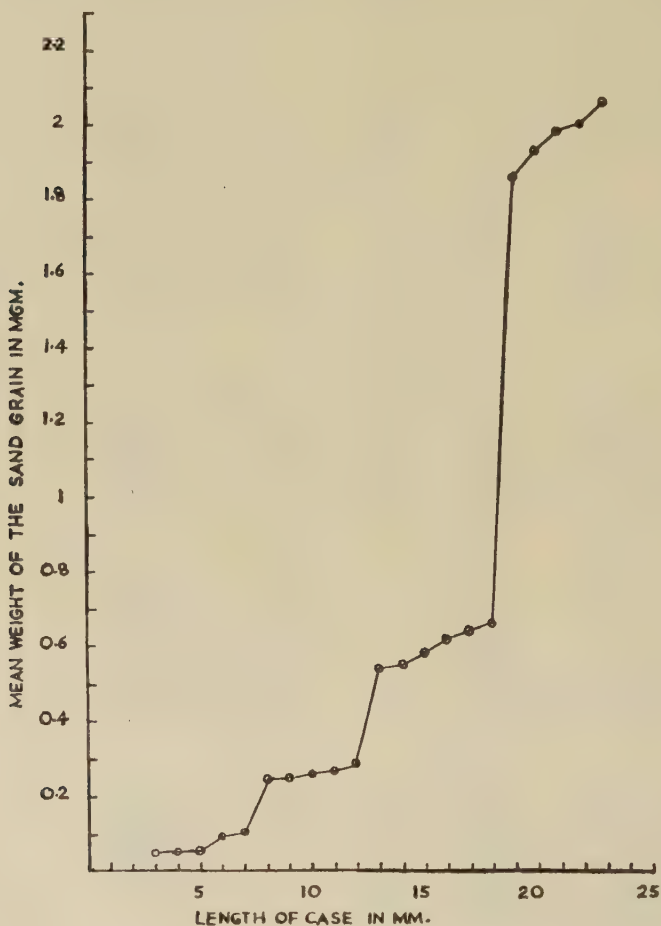

Fig. 2.—The relation between weight of sand grain and length of larval case
of *Potamophylax stellatus* (Curtis).

(b) *Limnephilus fuscicornis, Potamophylax stellatus* and *Chaetopteryx villosa.*—At certain stages the larvae used larger sand grains (fig. 2), which suggests that larvae of the same instar used grains of the same size. In order to prove this the head widths of eighty-one larvae of *P. stellatus* were measured ; these measurements are illustrated in figure 3. From this it is clear that the larvae fall into four instars (probably second to fifth). These larvae measured 1·4–6 mm., 7–10 mm., 11–17 mm. and 18–22 mm. in length and their cases 3–8, 9–11, 12–19, and 20–24 mm. in length. These case measurements nearly coincide with those of the cases in the four steps of the graph forming figure 2. This shows that larvae of the same instar select the same size of sand grains for building their cases.

(c) *L. centralis* and *L. vittatus*.—The larvae used progressively larger sand grains until they were nearly fully grown and thereafter the size was smaller (fig. 4).

DISCUSSION

From the above observations it appears that the quality, size and shape of the material are the three main factors that play an important role in its selection for building caddis cases. These factors will be discussed separately.

As far as the quality of materials is concerned, the species studied fall into four groups :
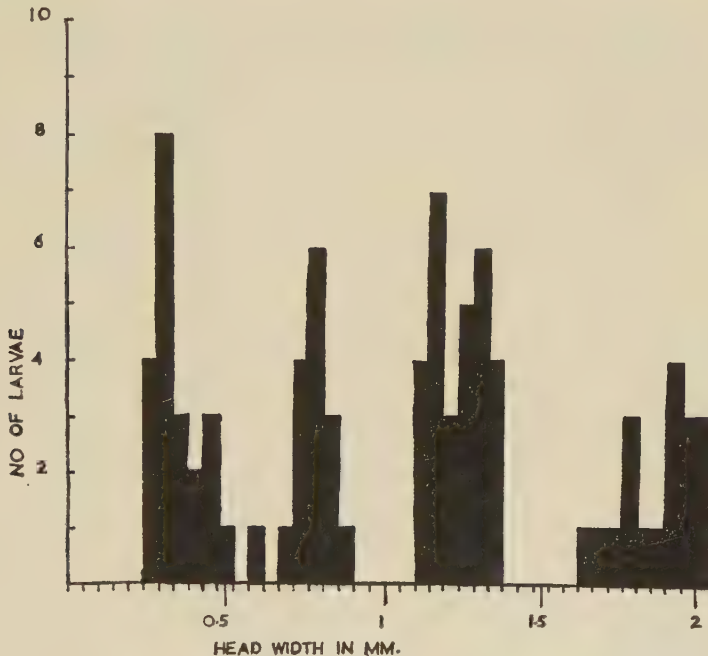

FIG. 3.—The relation between head width and number of *Potamophylax stellatus* (Curtis) larvae.

Group 1.—The following preferred the same kind of material throughout larval life :

> *Trichostegia minor, Agrypnia pagetana, Glyphotaelius pellucidus, Limnephilus flavicornis, L. centralis, L. vittatus, L. fuscicornis, Halesus radiatus* (Curt.), *Drusus annulatus* (Steph.), *Apatania muliebris* (McLach.), *Sericostoma personatum, Notidobia ciliaris, Goëra pilosa* (F.), *Silo nigricornis, Beraeodes minuta* (L.), *Molanna angustata, Odontocerum albicorne* (Scop.), *Athripsodes aterrimus* (Steph.) *Mystacides nigra* (L.), *Triaenodes bicolor* (Curt.), *Oecetis lacustris* (Pictet), *Athripsodes cinerea, Agapetus fuscipes* Curt. and *Glossosoma boltoni* Curt.

Group 2.—The following preferred a particular material when young and a different one when older :

> *Phryganea varia, Oligotricha ruficrus, Phryganea grandis, P. striata* L., *Brachycentrus subnubilus* Curt., *Crunoecia irrorata* (Curt.) and *Lepidostoma hirtum* (Fab.).

Group 3.—Young larvae of the following species built their cases of a mixture of materials, but, as they grew, they limited their choice to a particular material :

> *Potamophylax stellatus, P. latipennis* (Curt.), *Chaetopteryx villosa* and *Anabolia nervosa* (Curt.).

Group 4.—This group showed no clear preference. It contains only a single species, *Limnephilus lunatus* Curt.

Experiments with young larvae of *Agrypnia pagetana, Oligotricha ruficrus, Phryganea varia, P. grandis* and *P. striata* showed that they continued to build irregular cases, even when compelled to build new cases five to eight times. This seems to indicate an inherent lack of skill in building and it is only when older that they are able to build a neat case. Wesenberg-Lund (1911) suggested that the larvae of *P. grandis* may learn to build neater cases as they grow older.
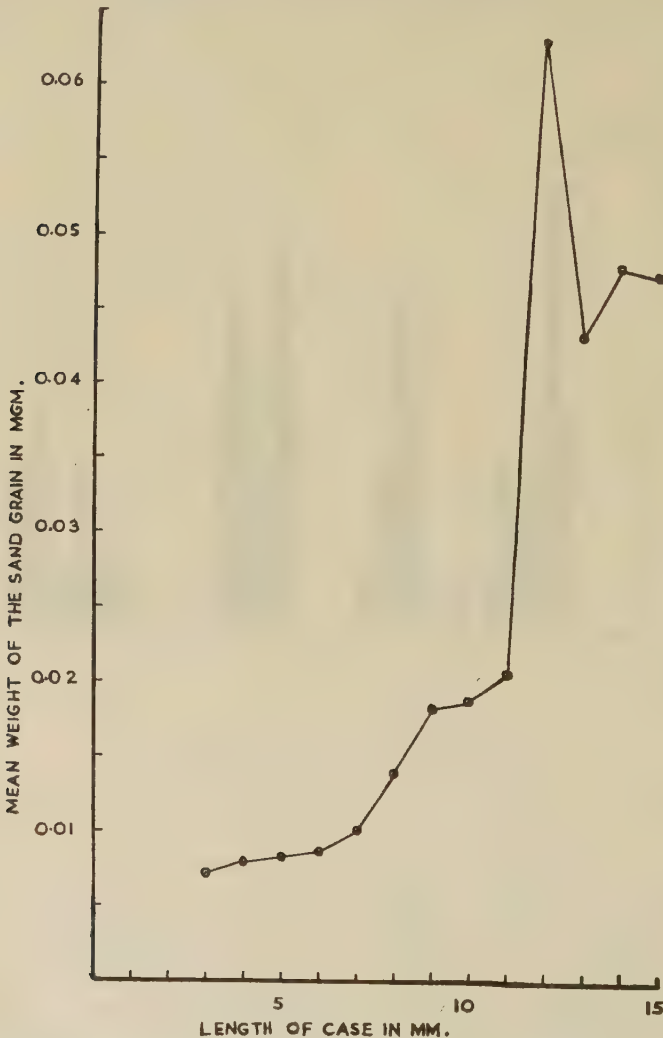

FIG. 4.—The relation between weight of sand grain and length of larval case of *Limnephilus centralis* Curtis.

My observations show that in all the species studied that built cases of sand grains, except *Agapetus fuscipes*, there was selection of definite size of grains. The larvae of *A. fuscipes* used sand grains of all sizes.

The larvae of *Glyphotaelius pellucidus* selected large pieces of leaves for the dorsal and ventral surfaces and small pieces for the sides. Larvae of *Goëra pilosa* and *S. nigricornis* selected small stones for the sides and large sand grains for the tubular portion. *Molanna angustata* selected larger sand grains for the wings than for the tubular part.

Apatania muliebris also selected large sand grains for the sides of the case and for the edges of the hood. *B. subnubilus*, *Crunoecia irrorata* and *Lepidostoma hirtum* selected equal lengths of material or cut larger pieces to size.

The larvae of *Glyphotaelius pellucidus* selected rounded flat pieces of dead leaves for building the dorsal and ventral surfaces of the case. *Limnephilus flavicornis* larvae preferred chips of plant materials ; those of *Potamophylax stellatus*, *P. latipennis* and *Chaetopteryx villosa* selected flattened pieces of grit. Although the larvae of *Sericostoma personatum*, *N. ciliaris* and *Odontocerum albicorne* used different shapes of sand grains, they always chose flattened ones and so produced the smooth surface of their cases.

The larvae of *Crunoecia irrorata* and *Lepidostoma hirtum* cut their material into rectangular pieces. In *Goëra pilosa* and *Silo nigricornis* the side stones are nearly flat on their ventral surface, while the dorsal surface is often rough. The inner surfaces of these stones are nearly straight, while the outer surfaces are mostly convex. Larvae of *Agapetus fuscipes* selected sharp-edged sand grains and stones, whereas those of *Glossosoma boltoni* selected flattened stones for building the sides of their cases.

Effect of selection of materials on distribution of larvae

(A) *Larvae that build cases of plant material*

These larvae preferred a specific material but in its absence built their cases from other plant material in a definite order of preference. Specimens of all these species were able to build cases of sand in the absence of plant materials, but many full grown larvae were unable to do so unless a little plant material was supplied.

As the larvae of this group can build of any plant material in the absence of that normally preferred, it is reasonable to suggest that case-building will not limit their distribution to certain ponds. This probably explains the varying composition of the cases of larvae of the same species in different ponds or even in different areas of the same pond.

Neave (1933) studied the distribution of *Phryganea cinerea* Walker in Lake Winnipeg. He found larvae throughout the length of the lake, and considered that the construction of the case reflected the conditions under which the larvae existed. Near the shore and in rivers bits of wood were used, and the case was built in the spiral manner characteristic of other species of the genus. Further out, these materials were not available, except accidentally, and the larva utilised an extraordinary assortment of materials which occurred naturally at the bottom or had fallen from the surface.

(B) *Larvae that build cases of sand grains*

These larvae fall into two groups :

(1) Larvae which use plant material in the absence of sand grains : *Limnephilus centralis*, *L. vittatus*, *L. fuscicornis*, *Potamophylax stellatus*, *P. latipennis*, *Chaetopteryx villosa*, *D. annulatus*, *Mystacides nigra*, *M. longicornis* L., young larvae of *Crunoecia irrorata* and *Lepidostoma hirtum*.

(2) Larvae which do not use plant material : *Apatania muliebris*, *Sericostoma personatum*, *N. ciliaris*, *Goëra pilosa*, *Silo nigricornis*, *Beraea maurus*, *Beraeodes minuta*, *Molanna angustata*, *O. albicorne*, *Athripsodes cinerea*, *Oecetis lacustris*, *Agapetus fuscipes* and *Glossosoma boltoni*.

These larvae are specialised, and in my experience they are found only in habitats where sand is available.

Neave (1933) studied the distribution of *Molanna flavicornis* Banks in Lake Winnipeg. He found that the larvae occurred in greatest numbers on a sandy bottom and also suggested that the size of sand grains in a particular area might be a factor limiting the distribution of this species.

Hickin (1946) described the habitat of *Molanna angustata*. He said " This caddis is a widely-distributed species, occurring commonly where its typical larval habitat is found. The latter consists of lakes, pools and slow moving rivers and streams with a bottom consisting of patches of sand and light gravel." My observations confirm those of Hickin.

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BOOK NOTICES

Ten Little Housemates. By K. VON FRISCH. 8vo. Pergamon Press, 1960. Pp. 146, text illust., 17s. 6d.

This work is a light hearted presentation of the structure and life of a varied selection of small creatures which, on occasions, leave their natural surroundings and enter houses. There are chapters on flies, gnats, bugs, lice, clothes moths, cockroaches, silverfish, spiders and ticks.

The book is not intended to be either an encyclopedia or a text-book, but merely to give information about familiar creatures. It is written in simple non-technical language.

Forest and shade tree entomology. By R. F. ANDERSON. 8vo. John Wiley & Sons, Inc., 1960. Pp. vii, 428 ; text illust., 68s.

This work is designed as a text-book and guide to the scientific understanding, identification and control of forest insects for students of forestry and entomology. It provides information both on basic principles and individual insect species and problems. To deal with these two subjects the volume is divided into two sections.

The first section presents the general principles of tree, forest and wood product entomology, with chapters on insect structure, physiology, development, classification, control methods, ecology, including the use of insecticides and surveys, and provides a background for the understanding of particular insect types and problems.

In section II the more important insect pests of forest and shade trees in North America are discussed and described. Information is given for each species on its hosts, distribution, appearance, life cycle and on the relative efficiency of available control methods. This section is designed to provide a quick, accurate means of identification of insect types by observation of the insect and examination of tree damage.

The work contains photographs, line drawings and tables, also a host and a general index.

PUBLICATIONS

The principal Publications of the Royal Entomological Society are *Transactions* and *Proceedings*.

The **Transactions** form an annual volume, each paper in the volume being issued as a separate part. The parts are issued irregularly throughout the year.

The **Proceedings** are issued in three series :

> Series A.   **General Entomology**
> Series B.   **Taxonomy**
> Series C.   **Journal of Meetings**

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The following information is supplied for the guidance of authors wishing to submit papers for publication in any of the Society's journals.

TRANSACTIONS

Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for illustrations to be in the hands of the Registrar as early as possible. Papers received *after* 1st April and 1st October cannot be considered at the meeting immediately following.

The Society is prepared to undertake the provision of a reasonable number of figures, in line or half-tone. Colour work is accepted only by special arrangement.

Papers of less than eight printed pages (approximately 5,000 words) will not normally be accepted for the *Transactions* and papers by authors who are not Fellows of the Society must be communicated by a Fellow.

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Papers submitted for publication in either *Series A* or *Series B* of the *Proceedings* are considered by the Editor and may be submitted at any time. Papers by authors who are not Fellows of the Society may be accepted if they are communicated by a Fellow.

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PROCEEDINGS SERIES C

Series C is issued before every General Meeting. It contains abstracts of communications to be made, together with the titles of papers accepted for publication in the *Transactions*.

The annual subscription to *Series A, General Entomology*, is £2 8s. 0d. ; *Series B, Taxonomy*, £2 8s. 0d. ; and *Series C, Journal of Meetings*, £1 0s. 0d.

As from January, 1936, the journal *Stylops* is continued as *Proceedings Series B, Taxonomy*. Copies of volumes 1–4 are available at £1 16s. 0d. each, post free.

GENERAL

The original drawings for all figures must be supplied by authors and must be drawn to a scale which will permit of their reduction, singly or after grouping, to an area of dimensions not exceeding 7 by 5 in.

A uniform method is adopted for the citation of bibliographical references in the Society's publications as follows :

> SMITH, A., 1936, New species of Coccidae. *Proc. R. ent. Soc. Lond.* (B) 6 : 301–6, pl. 1.
> —— 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* 84 : 901–36.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals, 3rd edition*, 1952.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

Papers offered for publication should be sent to the Registrar, Royal Entomological Society of London, at 41, *Queen's Gate, London, S.W.*7, and must be typewritten on one side of the paper only, with double spacing. **All papers in the Transactions must be provided with a summary.**

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MEETINGS

TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1961

Wednesday, May 3
       ,,   June 7
       ,,   July 5

THE ROYAL ENTOMOLOGICAL
SOCIETY OF LONDON

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Fellows and others wishing to make a communication to a General Meeting of the Society are requested to send in their names, the title of their exhibit, and a short abstract of their remarks, to the Hon. Secretary fourteen days before the meeting at which it is proposed to make the communication. Should it be desirable to publish a fuller account of the communication the manuscript may be submitted for publication in *Proceedings Series A* or *Series B*.

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